Tracking auditory processing and emotional response to music using EEG

Thesis (cumulative thesis)

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Summary

Auditory processing in humans is interwoven with affective processes. At this intersection, this thesis aims at determining the contribution of processing stages and components by using EEG.

The first part investigates tone processing in subjects with absolute pitch (AP). Until now active tasks have been used leaving it unclear how two particular mechanisms contribute to AP during passive listening. Based on a passive oddball paradigm, the present work investigated the electrophysiological dynamics underlying passive tone processing. Results reinforce the current opinion that early pitch memory is comparable among AP and Non-AP participants, whereas a later-occurring cognitive mechanism is critical for AP. Results are interpreted as reflecting cognitive facilitation in AP participants, possibly driven by the availability of multiple codes for tones.

The second part gains insights into music-evoked emotions. EEG was recorded from subjects while excerpts were presented. Independent component analysis in combination with cluster analysis revealed 10 clusters referring to brain areas involved in music and emotion processing. The results are partly compatible with the Heller's model, arguing that the frontal lobe is involved in modulating valence whereas the right parieto-temporal region contributes to arousal.

Focusing on affective processes in AP is promising for future research that might reveal insights into the cognitive-affective development in connection with brain plasticity.

Zusammenfassung

Beim Menschen ist die auditive Verarbeitung mit affektiven Prozessen verwoben. Diese Schnittstelle bildet der Ausgangspunkt dieser Dissertation, wobei Ziel ist, mit Hilfe von EEG Verarbeitungsstadien und Komponenten aufzuklären.

Der erste Teil untersucht die Tonverarbeitung von Absoluthörern (AH). Bisher wurden aktive Paradigmen verwendet, weshalb unklar bleibt, wie sich zwei bestimmte Verarbeitungsstufen während des passiven Hörens verhalten. Mittels passiven Paradigmas untersucht Studie 1 die zugrundeliegende elektrophysiologische Dynamik. Ergebnisse unterstützen die Theorie, dass AH und Nicht-AH bezüglich des frühen Tongedächtnisses vergleichbar seien und ein kognitiver Vorgang für das absolute Gehör verantwortlich sei. Die Befunde werden als kognitive Erleichterung interpretiert, die möglicherweise durch die Verfügbarkeit einer Mehrfachkodierung einzelner Töne unterstützt wird.

Der zweite Teil untersucht Musik-induzierte Emotionen. Probanden wurden einer EEG unterzogen, während ihnen Auszüge präsentiert wurden. Mittels Unabhängigkeits- und Clusteranalyse wurden 10 Cluster identifiziert, die an der Verarbeitung von Musik/Emotionen involviert sind. Die Befunde sind teilweise mit Heller's Modell kompatibel, das davon ausgeht, dass Valenz vom Frontallappen und Erregung von der rechten parieto-temporalen Region gesteuert werde.

Die Erforschung von affektiven Prozessen bei AH könnte wichtige Aufschlüsse über die kognitive-affektive Entwicklung im Rahmen der Plastizität liefern.

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1. Background and aims

The auditory system plays a pivotal role in signal processing, contributing to survival in that it enables communication and interaction with the environment. Auditory processing in humans is strongly interwoven with affective processes, which is not only reflected in language (i.e., semantics) or speech (i.e., prosody) but also in music perception. At this anthropologically revealing intersection, this thesis aims at tracking early processing stages and components by using electroencephalography (EEG).

The first part of this thesis (study 1) investigates tone processing in special subjects representing a bend point in auditory performance, namely in musicians with absolute pitch (AP). While focusing on passive tone listening, this study aims at determining the contribution of perceptual and cognitive mechanisms on the ability of AP. Whereas this study addresses a specific population, the second part (study 2) gains insights from the general population into a universal phenomenon, namely into emotions in the context of music listening. The goal of study 2 is to capture brain processes underlying emotions during natural music listening. In particular, it aims at revealing functionally distinct EEG sources contributing to valence and emotional arousal.

In the following, I will introduce the two subjects of research and the method used in these studies.

1.1 Absolute pitch (AP)

AP is defined as the rare ability to identify the chroma (pitch class) of a tone or to produce a specific pitch without the aid of any reference tones (Baggaley, 1974; Takeuchi & Hulse, 1993), a phenomenon that is almost only present in musicians (Deutsch, Dooley, Henthorn, & Head, 2009). Currently, its prevalence is estimated to be 1% at most, whereby subjects of Asian descent speaking tonal languages have a higher incidence rate (Deutsch, Henthorn, Marvin, & Xu, 2006, Deutsch et al., 2006; Deutsch, Li, & Shen, 2013; Gregersen, Kowalsky, Kohn, & Marvin, 1999).

There is evidence showing that both genetic and environmental factors contribute to the acquisition of AP (Athos et al., 2007; Baharloo, Johnston, Service, Gitschier, & Freimer, 1998; Baharloo, Service, Risch, Gitschier, & Freimer, 2000;

Gregersen et al., 1999; Theusch, Basu, & Gitschier, 2009). The latter factor includes early language exposure (Deutsch, Henthorn, & Dolson, 2004a, Deutsch, Henthorn, & Dolson, 2004b; Deutsch et al., 2006), the nature of musical training and exposure to music during childhood (Gregersen, Kowalsky, Kohn, & Marvin, 2001). There is also evidence for a sensitive period during which these environmental inputs determine the emergence of AP (Gervain et al., 2013; Miyazaki, 1988; Russo, Windell, & Cuddy, 2003). In fact, previous studies revealed that the earlier one begins with musical training, the more likely it is to develop AP (Deutsch et al., 2006; Gregersen et al., 2001; Meyer et al., 2011).

According to current knowledge, at least two differential processing stages contribute to the ability of AP (Levitin, 1994; Levitin & Rogers, 2005; Zatorre, 2003). The first one reflects the early phase of pitch encoding at the processing level of the auditory-related cortex, and refers to pitch memory within fixed tone categories. The second one is assumed to rely on conditional associative memory mechanisms and to be driven by the association between categorized pitches and verbal labels or other abstract codes (Zatorre & Beckett, 1989). These memory associations are assumed to be acquired as a function of musical training and music exposure during the sensitive period (Miyazaki, 1988; Russo et al., 2003; Zatorre, 2003). Until now, several studies have provided evidence for both processing stages.

Despite its low incidence rate, this specific type of hearing has turned out to be evolutionary conserved (Hauser & McDermott, 2003) and to be temporarily dominant during infancy (Saffran & Griepentrog, 2001), suggesting that it has behavioral significance. Research on AP has already successfully contributed to a better understanding of perceptual expertise and memory functions (Burns & Campbell, 1994; Levitin & Rogers, 2005). Currently, scientists agree that AP can serve as a reasonable model to better understand several topics such as plasticity in the auditory system or interactions between experiential, maturational and genetic factors during general cognitive development (Zatorre, 2003).

1.2 Music and emotions

Behavior somehow related to music is present in various species across taxonomic groups (e.g., humpback whales, gibbons, songbirds) (Gray et al., 2001; Geissmann, 2002). However, only humans exhibit music appreciation, a

phenomenon beyond music-related behavior underlying mating or territorial functions. This unique phenomenon is of anthropological significance that is reflected in music's omnipresence not only across cultures but also across human history. A big body of archeological findings (e.g., bone and ivory flutes) dating back to the middle palaeolithic period strongly suggests that in prehistorian time humans (and likely the homo neanderthalensis) must have already been involved in sophisticated music (Conard et al. 2009; Gray et al., 2001). Music involvement not only accompanies humans since the beginning of mankind but also encounters each individual at the beginning of lifespan as reflected in infant's rhythmic engagement and in parent–child singing (Zentner & Eerola, 2010; Trehub, 2003), a universal serving pre-linguistic communication and emotion regulation. In fact, human's main motivation for listening to music is to regulate affective states (Panksepp, 1995; Juslin & Laukka, 2004). Music has the power to induce pleasure and related reward experiences, this mainly contributing to the phenomenon of music appreciation. Similarly to other reward-related behaviors (e.g., mating, feeding), pleasure induced by music recruits the striatal dopaminergic system (Blood et al., 1999; Blood & Zatorre, 2001; Brown et al., 2004; Menon & Levitin, 2005; Salimpoor et al., 2011, 2013), reinforcing music-listening behavior. However even though music listening appears to be driven by an evolutionary conserved mechanism, yet no impact on sexual fitness is known.

Experience during music listening goes beyond (dis)pleasure, involving neocortical areas (Zatorre et al., 2007; Salimpoor et al., 2013; Zatorre & Salimpoor, 2013) that enable emergence of more complex and music-specific (so-called "aesthetic"; Scherer, 2004) emotions. In addition, musical experience alone, regardless of the musical stimulus, varies enormously across humans, partly reflecting the variety of the shaping environment permits. Due to this complexity and variability, research in the domain of music-induced emotions is rather challenging.

In fact, the challenge already starts at the conceptual level, namely in defining "emotions". Different disciplines dealing with emotions, especially in response to music, seem not to have "complementary views of the same phenomenon, but divergent views on substantively different phenomena" (Konečni, 2003). Thus, a fruitful basis for a working definition relies on a componential approach proposing that an emotion episode consists of coordinated (i.e., synchronized) changes in three major reaction components: physiological arousal, motor expression, and subjective

feelings (Scherer, 2004). Currently, different models on emotions are suggested, leading to various scopes of capture. The commonly used emotion models are the two-dimensional circumplex model (comprising the orthogonal dimensions of valence and arousal; Russell, 1980), the discrete emotion model (i.e., basic emotions such as such as fear, anger, disgust, sadness and happiness; Ekman, 1992) and the domain-specific emotion model specifically dedicated to music-induced emotions (i.e., wonder, transcendence, tenderness, nostalgia, peacefulness, power, joyful activation, tension and sadness; Zentner, Grandjean, Scherer, 2008).

1.3 Electroencephalography (EEG)

EEG is a powerful noninvasive technique, frequently applied in the field of psychology and neuroscience. It enables to record brain activity in terms voltage fluctuations between active electrodes and a reference electrode. In other words, it represents the differences in voltage (μV) between different cerebral locations plotted over time (ms). The EEG signal is recorded on the scalp surface, and reflects the summed postsynaptic activity, primarily generated by the large vertically oriented pyramidal neurons especially in the cortical layers III, V, and VI (Olejniczak, 2006). Since it provides nearly real-time measurements, it constitutes a promising approach to gain insights into psychological processes. Several approaches exist to capture brain stages and temporal brain dynamics during processing.

1.3.1 Event-related potentials (ERP)

One of the most common EEG approach is ERP analysis. By repeatedly exposing the brain to specific time-locked events (e.g., stimulus, concept, task or mental condition) and then averaging the EEG responses, one can disentangle the event-related signal from the event-unrelated one that gets averaged out. ERPs can be studied as specific components that feature specific latencies, polarities, scalp distributions, and are related to specific functions. In study 1, two ERP components are used for investigation. Firstly, the Mismatch Negativity (MMN), a negative-going brain response elicited at about 100–250 msec after stimulus onset in response to a detectable change within a repetitive stream of auditory stimuli (Näätänen, 2000; Näätänen, Gaillard, & Mäntysalo, 1978). The MMN is assumed to have its major

sources is located in the auditory cortex and reflect pre-attentive auditory processing (Garrido, Kilner, Stephan, & Friston, 2009; Picton, Alain, Otten, Ritter, & Achim, 2000). Secondly, the P3a, a brain response that occurs subsequently to the MMN, and is characterized by a positive-going deflection peaking at about 300 msec post-stimulus onset, with a maximal current distribution over fronto-central scalp sites (Kujala, Tervaniemi, & Schröger, 2007; Escera, Alho, Schröger, & Winkler, 2000). This component is linked to a range of cognitive processes underlying an attentional resource allocation. The P3a originates from stimulus-driven frontal (phasic) attentional mechanisms (Polich, 2007; Squires, Squires, & Hillyard, 1975), indexes involuntary orienting of attention (Escera et al., 2000), and reflects attentional distraction (Comerchero & Polich, 1999) and novelty processing (Friedman, Cycowicz, & Gaeta, 2001; Knight, 1996). It stems from a distributed limbic-cortical circuit (Knight & Nakada, 1998; Knight, 1984, 1996; Knight, Grabowecky, & Scabini, 1995), also including a multimodal brain region, namely the temporal–parietal junction (Knight, Scabini, Woods, & Clayworth, 1989).

1.3.2 Independent component analysis (ICA)

EEG data directly derived from the scalp is consisted of a mixture of multiple cortical sources, requiring caution in interpretation. ICA is a powerful method that unmixes EEG data into independent components (ICs) contributing to functionally distinct brain processes. This method determines the “unmixing” matrix W with which it unmixes the multi-channel EEG data X into a matrix U comprising the channel-weighted sum of statistically IC activity time courses. Thus, U = WX.

Whereas the ERP technique is indicated for research allowing highly controlled and repetitive experimental settings, ICA is a promising data-driven approach used to investigate states during more ecologically valid real-world experiences. From complex brain activities, ICA allows to “blindly” determine distinct neural sources with independent time courses associated with features of interest while still ensuring an optimal signal-to-noise ratio (Jutten & Herault, 1991; Makeig et al., 1996; Makeig et al., 1997; Makeig et al., 2000; Jung et al., 2001; Makeig et al., 2004; Lemm et al., 2006). This approach is used in study 2 to capture brain processes underlying emotions during natural music listening. So far, ICA has already been proved to be fruitful in gaining insights into natural music processing

(Schmithorst, 2005; Sridharan et al., 2007; Lin et al., 2010; Cong et al., 2013; Cong et al., 2014; Lin et al., 2014), but additionally in other real-world conditions such as resting state (Damoiseaux et al., 2006; Mantini et al., 2007; Jancke & Alahmadi, 2015), natural film watching (Bartels & Zeki, 2004, 2005; Malinen et al., 2007) and the riddle of the cocktail party effect (Bell & Sejnowski, 1995).

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2. Empirical part

2.1 Overview

Study 1

Absolute Pitch: Evidence for Early Cognitive Facilitation during Passive Listening as Revealed by Reduced P3a Amplitudes

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Study 2

Independent component processes underlying emotions during natural music listening

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2.2 Study 1: Absolute Pitch: Evidence for Early Cognitive Facilitation during Passive Listening as Revealed by Reduced P3a Amplitudes

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2.2.1 Abstract

Absolute pitch (AP) is the rare ability to identify or produce different pitches without using reference tones. At least two sequential processing stages are assumed to contribute to this phenomenon. The first recruits a pitch memory mechanism at an early stage of auditory processing, whereas the second is driven by a later cognitive mechanism (pitch labeling). Several investigations have used active tasks, but it is unclear how these two mechanisms contribute to AP during passive listening. The present work investigated the temporal dynamics of tone processing in AP and non-AP (NAP) participants by using EEG. We applied a passive oddball paradigm with between- and within tone category manipulations and analyzed the MMN reflecting the early stage of auditory processing and the P3a response reflecting the later cognitive mechanism during the second processing stage. Results did not reveal between-group differences in MMN waveforms. By contrast, the P3a response was specifically associated with AP and sensitive to the processing of different pitch types. Specifically, AP participants exhibited smaller P3a amplitudes, especially in between-tone category conditions, and P3a responses correlated significantly with the age of commencement of musical training, suggesting an influence of early musical exposure on AP. Our results reinforce the current opinion that the representation of pitches at the processing level of the auditory-related cortex is comparable among AP and NAP participants, whereas the later processing stage is critical for AP. Results are interpreted as reflecting cognitive facilitation in AP participants, possibly driven by the availability of multiple codes for tones.

2.2.2 Introduction

Music perception relies principally on understanding tone relations. Therefore, music tuition primarily aims at promoting a well-developed relative pitch (RP), meaning the ability to identify or produce tone intervals (Takeuchi & Hulse, 1993). Most interestingly, there are only a few humans who are able to categorize pitches effortlessly. Such individuals possess the rare ability called absolute (or perfect) pitch (AP), which is defined as the ability to identify the chroma (pitch class) of a tone or to produce a specific pitch without the aid of any reference tones (Levitin & Rogers, 2005; Zatorre, 2003; Takeuchi & Hulse, 1993; Baggaley, 1974). This rare ability

occurs in less than 1% of the general population (Takeuchi & Hulse, 1993), whereby Asian people speaking tonal languages have a higher incidence rate of AP (Deutsch, Li, & Shen, 2013; Deutsch, Dooley, Henthorn, & Head, 2009; Deutsch, Henthorn, Marvin, & Xu, 2006; Deutsch, Henthorn, & Dolson, 2004a; Gregersen, Kowalsky, Kohn, & Marvin, 1999). Interestingly, whereas most of the AP possessors are musicians (Deutsch et al., 2009), a handful of them possess AP in terms of a savant skill in the context of autism (Brenton, Devries, Barton, Minnich, & Sokol, 2008; Heaton, Davis, & Happé, 2008) or Williams syndrome (Lenhoff, Perales, & Hickok, 2001). Although hearing absolutely appears to be a rare phenomenon, it is the more fundamental and rudimental cognitive feature than relational hearing (Levitin & Rogers, 2005). This view is supported by findings on infants preferring absolute over relative cues in auditory-based tasks (Saffran & Griepentrog, 2001) and by evolutionary research suggesting that RP is the more recent ability that emerged only after the divergence between birds and mammals (Hauser & McDermott, 2003). Meanwhile, there is evidence showing that both genetic and environmental factors contribute to the acquisition of AP (Theusch, Basu, & Gitschier, 2009; Athos et al., 2007; Baharloo, Service, Risch, Gitschier, & Freimer, 2000; Gregersen et al., 1999; Baharloo, Johnston, Service, Gitschier, & Freimer, 1998). The latter includes learning factors such as early language exposure (Deutsch et al., 2004a, 2006; Deutsch, Henthorn, & Dolson, 2004b) and the nature of musical training and exposure to music during childhood (Gregersen, Kowalsky, Kohn, & Marvin, 2001). In a similar manner as for language acquisition, there is likewise evidence for a sensitive period during which these environmental inputs determine the emergence of AP (Gervain et al., 2013; Russo, Windell, &Cuddy, 2003; Miyazaki, 1988). This evidence shows that the earlier one begins with musical training, the more likely it is to develop AP (Meyer et al., 2011; Deutsch et al., 2006; Gregersen et al., 2001). According to current knowledge, at least two separable processing stages have been proposed to contribute to the ability of AP (Schulze, Mueller, & Koelsch, 2013; Levitin & Rogers, 2005; Zatorre, 2003; Levitin, 1994; Deutsch, 1987). The first one reflects the early phase of pitch encoding at the processing level of the auditory-related cortex (“pitch memory”) and refers to pitch memory within fixed categories. The second processing stage (“pitch labeling”) is assumed to rely on a conditional associative memory mechanism and to be driven by the association of categorized pitches with verbal labels or other abstract codes (Zatorre & Beckett, 1989). Normally, these memory

associations are acquired as a function of musical training and music exposure during the sensitive period (Russo et al., 2003; Zatorre, 2003; Miyazaki, 1988). Some evidence supporting the hypothesis that the first processing stage operates differently in AP musicians has been provided by previous studies indicating that AP participants perceive tones more categorically (Schulze et al., 2013; Siegel, 1974), meaning that they encode tones within narrower pitch categories (Zatorre, 2003). In this context, AP participants were shown to exhibit altered neurophysiological responses during early stages of auditory processing (Matsuda et al., 2013; Schulze, Gaab, & Schlaug, 2009; Wu, Kirk, Hamm, & Lim, 2008; Itoh, Suwazono, Arao, Miyazaki, & Nakada, 2005; Ohnishi et al., 2001; Hirata, Kuriki, & Pantev, 1999). In addition, there is some evidence pointing to a differential structural architecture in the brain networks of AP participants involved in the early stage of auditory processing (Wengenroth et al., 2013; Jäncke, Langer, & Hänggi, 2012; Loui, Zamm, & Schlaug, 2012; Loui, Li, Hohmann, & Schlaug, 2011; Oechslin, Imfeld, Loenneker, Meyer, & Jäncke, 2010; Bermudez, Lerch, Evans, & Zatorre, 2009; Wilson, Lusher, Wan, Dudgeon, & Reutens, 2009; Luders, Gaser, Jancke, & Schlaug, 2004; Keenan, Thangaraj, Halpern, & Schlaug, 2001; Schlaug, 2001; Schlaug, Jancke, Huang, & Steinmetz, 1995). Nevertheless, to date it is still a matter of debate whether the specificity of the first processing stage is restricted to AP participants only. In fact, individuals without AP also possess the rudimentary ability to memorize pitches. This has been observed, for example, when nonmusicians have to produce songs from memory (Jakubowski & Müllensiefen, 2013; Levitin, 1994) or to judge the correctness of familiar soundtracks (Schellenberg & Trehub, 2003) or even telephone dial tones (Smith & Schmuckler, 2008). In the same vein, recent evidence indicates that mental representations of tone categories in AP participants are not fixed but rather changeable (Hedger, Heald, & Nusbaum, 2013; McLachlan, Marco, & Wilson, 2013), implying a certain extent of instability. Taken together, these findings suggest that pitch memory per se does not seem to be specific for AP. Meanwhile, there is growing evidence supporting the view that the second processing stage is the crucial psychological process where AP musicians differ from non- AP (NAP) musicians (Elmer, Sollberger, Meyer, & Jäncke, 2013; Zatorre, Perry, Beckett, Westbury, & Evans, 1998; Crummer, Walton, Wayman, Hantz, & Frisina, 1994; Hantz, Crummer, Wayman,Walton, & Frisina, 1992; Wayman, Frisina, Walton, Hantz, & Crummer, 1992; Klein, Coles, & Donchin, 1984). Evidence pointing into this direction arises, for

example, from Zatorre et al. (1998), who could show that the left posterior dorsolateral pFC, a brain region involved in conditional associative learning (Petrides, Alivisatos, Evans, & Meyer, 1993; Petrides, 1990), is selectively recruited during tone listening in AP participants. In addition, previous anatomical studies pointed to a differential architecture in the posterior dorsal frontal region of AP participants compared with participants without AP (Bermudez et al., 2009; Bermudez & Zatorre, 2005). Further evidence indicating a cognitive mechanism underlying AP has been collected by using EEG, which constitutes a particularly advantageous technique for capturing temporal dynamics. In this context, previous EEG studies using active oddball paradigms revealed that AP is associated with a reduction or absence of the P300 component, probably reflecting more parsimonious memory processes (Crummer et al., 1994; Hantz et al., 1992; Wayman et al., 1992; Klein et al., 1984). Moreover, by using a conceptual association task, Elmer, Sollberger, et al. (2013) identified later-occurring cognitively related brain responses (N400 and LPC; Kutas & Federmeier, 2011; Friedman & Johnson, 2000) as reliable and specific markers for AP. Most of the published oddball studies (Crummer et al., 1994; Hantz et al., 1992; Wayman et al., 1992; Klein et al., 1984) used active tasks for evaluating AP. By contrast, to date only few oddball studies focused on passive listening paradigms (Matsuda et al., 2013; Meyer et al., 2011; Tervaniemi, Alho, Paavilainen, Sams, & Näätänen, 1993). Passive oddball paradigms are particularly fruitful in that they permit to determine the contribution of both mechanisms without potential contaminations of explicit top–down functions (Näätänen, Paavilainena, Rinned, & Alhod, 2007; Pulvermüller & Shtyrov, 2006). Until now, all passive oddball studies focused on MMN, which is a negative-going brain response elicited at about 100–250 msec after stimulus onset in response to a detectable change (deviation) within a repetitive stream of auditory stimuli (standard; Näätänen, 2000; Näätänen, Gaillard, & Mäntysalo, 1978). The MMN is assumed to reflect preattentive auditory memory at the processing level of the auditory-related cortex (Garrido, Kilner, Stephan, & Friston, 2009; Picton, Alain, Otten, Ritter, & Achim, 2000). By using a passive paradigm, Tervaniemi et al. (1993) did not find different MMN waveforms between participants with and without AP while processing tones. By contrast, Matsuda et al. (2013) reported larger MMN amplitudes in AP participants in response to mistuned tones. The same perspective is provided by Meyer et al. (2011), who demonstrated different MMN responses in Suzuki children with weak to moderate AP abilities.

Surprisingly, none of the previous EEG studies took advantage of the P3a response for measuring the contribution of cognitive functions to AP. This specific brain response is elicited in the context of oddball paradigms, occurs subsequently to the MMN, and is characterized by a positive-going deflection peaking at about 300 msec post-stimulus onset, with a maximal current distribution over frontocentral scalp sites (Kujala, Tervaniemi, & Schröger, 2007; Escera, Alho, Schröger, & Winkler, 2000). On the basis of the observation that P3a manifestations appear at a relatively late stage of cortical processing, this component has been linked to a range of cognitive processes underlying an attentional resource allocation. In fact, the P3a response originates from stimulus-driven frontal (phasic) attentional mechanisms (Polich, 2007; Squires, Squires, & Hillyard, 1975), indexes involuntary orienting of attention (Escera et al., 2000), and reflects attentional distraction (Comerchero & Polich, 1999) and novelty processing (Friedman, Cycowicz, & Gaeta, 2001; Knight, 1996). Interestingly, the P3a response stems from a distributed limbic-cortical circuit (Knight & Nakada, 1998; Knight, 1984, 1996; Knight, Grabowecky, & Scabini, 1995), also including a multimodal brain region, namely the temporal–parietal junction (Knight, Scabini, Woods, & Clayworth, 1989). Thus, this component has been shown to constitute a marker for assessing early multimodal processing (Jancke, Rogenmoser, Meyer, & Elmer, 2012; Boll & Berti, 2009). The latter point is of relevance, in that it permits to characterize the second processing stage of AP. This appears promising considering that AP participants are assumed to process tones multidimensionally by relying on multiple mental codes for tones (Hantz et al., 1992; Zatorre & Beckett, 1989; Klein et al., 1984). This specific view is supported by an older study of Zatorre et al. (1998) showing activation in brain areas involved in multimodal processing (bilateral middle and inferior temporal cortex). Although the specific cognitive processes reflected by the P3a, as well as its independence from the posterior P300 (P3b) component, are still a matter of debate (Polich, 2007), there is at least agreement that the P3a is linked to early cognitive processing during passive and attentive-free listening (Kujala et al., 2007; Escera et al., 2000).

In the present EEG study, we applied a passive oddball paradigm with between- and within-tone category manipulations and made use of the MMN and P3a components for reevaluating the two processing stages assumed to contribute to the ability of AP. In the case that AP is principally driven by a pitch memory mechanism occurring at the processing stage of the auditory-related cortex, one would expect

between-group differences in the MMN responses, especially in response to between-tone category manipulations. Alternatively, if this ability is due to a cognitive mechanism, effects are more likely to be associated with P3a responses.

2.2.3 Methods

2.2.3.1 Participants

Sixteen AP (four men, mean age = 25.4 years, *SD* = 9.6 years) and 10 NAP participants (two men, mean age = 24.4, *SD* = 3.0 years, all native German speakers) participated in this study. All AP (eight string players, eight pianists) and NAP participants (five string players, four pianists, and one flutist/pianist) were professional musicians and consistently right-handed (with the exception of two in the AP group and one in the NAP group who were left-handed), as revealed by the Edinburgh Handedness Inventory (Oldfield, 1971). None of them reported any history of present or past neurological, psychiatric, or audiological disorders, and all participants had an unremarkable audiological status, as revealed by pure tone audiometry (Home Audiometer software, www.esseraudio.com/de/homeaudiometer-hoertest.html). All participants denied consumption of illegal drugs or regular medication. The participants were paid for participation, the local ethics committee approved the study, and written informed consent was obtained from all participants.

2.2.3.2 History of musical training

History of musical training was assessed by an in-house questionnaire previously used by our research group (Elmer, Hänggi, Meyer, & Jäncke, 2013; Elmer, Sollberger, et al., 2013; Elmer, Meyer, & Jäncke, 2012). This questionnaire was adopted to evaluate the age of onset of musical practice, the primary instruments played by the musicians, the number of years of musical training, and the self-estimated number of training hours per week during every 3-year period of life. On the basis of the subjective data reported by the participants, the total number of training hours across lifespan was extrapolated for each participant.

2.2.3.3 Musical aptitude

To control for differences in musical aptitude between the two groups, all participants performed the Advanced Measures of Music Audition test (Gordon, 1989). This test consists of 30 successive trials in which the participants have to compare pairs of piano melodies and to decide whether these are equivalent, rhythmically different, or tonally different. On the basis of biographical information (history of musical training) and the Advanced Measures of Music Audition test, we estimated musical aptitude.

2.2.3.4 AP ability

To verify and quantify AP ability, the participants performed a pitch-labeling test previously used by our research group (Jancke et al., 2012; Oechslin, Imfeld, et al., 2010; Oechslin, Meyer, & Jäncke, 2010). During this test, participants listened to 108 pure sine wave tones presented in a pseudorandomized order and were instructed to write down the tonal label immediately after they heard the accordant tone. The tones ranged from A3 (tuning: A4 = 440 Hz) to A5 and were presented three times each, whereby same tones were never presented successively. Each tone presented during the test had a duration of 1 sec. The ISI had a duration of 4 sec and was filled with Brownian noise. The accuracy was evaluated by counting the total number of correct responses. Semitone errors were counted as incorrect responses to increase discriminatory power. However, participants were not asked to identify the adjacent octaves of the presented tones.

2.2.3.5 Cognitive capability

Between-group differences in intelligence were controlled by applying a short German intelligence test (Mehrfachwahl–Wortschatz Intelligenz Test [MWT-B]), which is frequently used in German-speaking countries as a standard test to measure psychometric intelligence (Lehrl, Triebig, & Fischer, 1995). This test permits to estimate crystalline intelligence in a short time and was previously shown to correlate fairly well (r = .72) with the global intelligence quotient in healthy adults (Lehrl et al.,

1995). The MWT-B consists of 37 items, which are ordered as a function of difficulty level. For each item, the participants had to choose the unique word with a meaning out of five pseudowords.

2.2.3.6 Stimuli and procedure

The auditory stimuli presented during EEG recording were five piano tones taken from the study of Jancke et al. (2012), namely, an A tone (fundamental frequency f0 = 440 Hz), a C tone (f0 = 264 Hz), an A-flat tone (f0 = 416 Hz), and two mistuned tones deviating from the A tone with different degrees. One of the mistuned tones had a frequency of 438 Hz (1/10-semitone deviation), whereas the other one had a frequency of 422 Hz (3/4-semitone deviation). All piano tones lasted 200 msec, were registered as 16-bit stereo files, matched for intensity by normalizing the amplitudes, and smoothed with a rise and fall time of 5 msec to avoid an abrupt decay. All these processing steps were performed by using Praat (www.fon.hum.uva.nl/praat/) and Adobe Audition 1.5. (tv.adobe.com/de/product/audition/). During EEG recording, all auditory stimuli were delivered binaurally with a sound pressure level of about 70 dB (Digital Sound Level Meter 329, Voltcraft) by using HiFi headphones (Sennheiser, HD 25-1, 70 Ω, Ireland).

During EEG measurements, participants were instructed to focus their attention on a silent film while ignoring the five piano tones, which were simultaneously presented. The experiment consisted of five different blocks randomly presented across all participants and the two groups. In each block, one of the five tones was presented frequently (standard tone), whereas the remaining four tones were presented occasionally (deviant tones). Each block consisted of 420 standard tones and 4 × 70 deviant tones. The standard tone had an occurrence probability of .6 and each deviant of .1. For EEG analyses, we focused only on the blocks in which tone A (block A) and tone C (block C) were presented as standard tones, because in these two conditions deviation levels increased or decreased unambiguously and EEG components could be studied as particular functions of deviation magnitude. Block A provides information concerning tone processing in response to within- and between-tone categories, whereas block C reflects extreme conditions in the context of between-tone categories only. The term “tone category” refers to the smallest musical tone interval used in Western music. Table 1 gives an overview of the study

design.

Table 1

Study Design

	Standard Tones (420x/ *p* = .6)	Deviant Tones (Each 70x/ *p* = .1)			
Block A	440 Hz	438 Hz	422 Hz	416 Hz	264 Hz
Block C	264 Hz	416 Hz	422 Hz	438 Hz	440 Hz

Deviant tones are listed from left to right according to deviation level. In block A the first 2 deviant tones differed within the category of the standard tone A, whereas the last 2 differed in terms of novel tone categories. In block C all deviant tones differed more than one category from standard tone C.

Each block started with a sequence of 15 successive standard tones, so that a stable memory trace could be established (Horváth, Czigler, Sussman, & Winkler, 2001; Näätänen & Winkler, 1999). After that, all tones were presented in a pseudorandomized order, whereby each deviant tone was followed by at least one standard tone, the same deviant tone was never presented successively, and at least two different tones were inserted before presenting again a specific deviant tone. The ISI was of 550 msec.

2.2.3.7 EEG recording

During EEG recording, the participants were placed in a chair at a distance of about 100 cm from a monitor. The EEG (32 channels, subset of the 10/10 system) was recorded with a sampling rate of 1000 Hz and a band pass filter from 0.1 to 100 Hz using an EEG amplifier (Brain Products, Munich, Germany). We applied sintered silver/silver-chloride electrodes (Ag/AgCl) and used the nose position as online reference. Electrode impedance was reduced to <10 kΩ by using Electrogel conductant.

2.2.3.8 Data analyses

2.2.3.8.1 Preprocessing

For all steps of digital EEG raw data processing, we used Brain Vision Analyser software (Version 2.02, Brain Products, Munich, Germany). The data were high- and lowpass filtered offline at 1–20 Hz, and artifacts were removed by using an independent component analysis (Jung et al., 2000) in association with a semiautomatic raw data inspection. For the eight deviant tones and the two standard tones (see Table 1), segments of 500-msec duration were created, including a 100-msec prestimulus period. Furthermore, a baseline correction relative to the −100 to 0 msec prestimulus time period was applied. All segments were averaged to compute ERPs. In a next processing step, the ERPs in response to the standard tones were subtracted from the ERPs elicited by the deviant tones (physically identical stimuli presented in different blocks). Furthermore, we computed multi-subject grand averages for each group and difference waves.

2.2.3.8.2 MMN and P3a calculation

In the present work, we specifically evaluated MMN and P3a responses (difference waves). On the basis of the voltage distribution over the scalp (see Figure 4) and to avoid multiple comparisons between neighboring electrodes as well as to increase the signal-to-noise ratio, nine frontal electrodes were pooled into one ROI (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, and C4; Jancke et al., 2012; Eichele, Nordby, Rimol, & Hugdahl, 2005). The time windows (TWs) used for analyzing the MMN and the P3a responses were defined separately for each group and deviant condition, according to two consecutive global field power minima of the corresponding grand averages. MMN and P3a amplitudes were selected for each single participant and condition by using a semiautomatic peak detection algorithm. The labeled peaks were additionally confirmed by visual inspection. Furthermore, the finding of a genuine MMN was validated by an inversion of polarity that became manifest at the lateral mastoid electrodes (TP9 and TP10). To verify the presence of MMN and P3a, the maximal amplitudes were statistically tested against zero by using one-sample t-

tests.

2.2.3.8.3 Statistical analyses

The amplitudes as well as the latencies of the MMN and P3a amplitudes were evaluated by using the SPSS software (SPSS 19 for Windows; www.spss.com). In particular, we computed 2 × 4 ANOVAs with a two-way grouping factor (Group: AP vs. NAP) and a four-way repeated measurement factor (Deviation: four deviation levels as reflected by difference waves). Statistical analyses were adjusted for nonsphericity using Greenhouse–Geisser Epsilon when equal variances could not be assumed. Significant interaction effects were further inspected by using post hoc *t*-tests. All post hoc *t*-tests were corrected for multiple comparisons by using the Bonferroni procedure (corrected $\alpha' < .05/4 = .0125$). Because it is important to report the strength of an effect independent of the sample size, we also calculated the effect size (ηp^2) by dividing the sums of squares for the effects by the sums of squares for these effects plus its associated error variance within the ANOVA study. Correlation analyses (Pearson product–moment correlation coefficient) were used for investigating potential relationships between electrophysiological and biographical data.

2.2.4 Results

2.2.4.1 Behavioral data

2.2.4.1.1 Biographical data, cognitive capability, and musical aptitude

The statistical evaluation of age, general cognitive capability, musical aptitude, age of onset of musical practice, total number of years of musical training, mean number of musical training hours per year, and the total number of musical training hours across lifespan did not reveal significant group differences. The results are listed in Table 2.

Table 2

Biographical data

	AP	NAP	*p*
Age (years)	25.4 (9.6)	24.4 (3.0)	.76
General cognitive capability[a]	29.4 (3.8)	30.0 (3.6)	.68
Musical aptitude[a]	67.6 (6.5)	66.0 (6.6)	.55
Age onset of musical practice (years)	4.6 (1.6)	5.8 (2.1)	.11
Total number of years of music training	21.1 (8.5)	18.7 (4.1)	.41
Mean training hours per year	670.5 (331.7)	493.5 (169.0)	.13
Total number of training hours across lifespan[b]	1.7 (1.1)	1.2 (.5)	.19

Listed are the means of the variables of both groups and the p values (*t*-tests). Standard deviations are reported in brackets. [a]Raw scores were used. [b]Unites are given in 1×10^4.

2.2.4.1.2 Pitch-labeling test

Participants who claimed to have AP scored considerably better on the pitch-labeling test (mean score = 79.6%, *SD* = 18.0%) than participants who claimed to not have AP (mean score = 8.4%, *SD* = 5.4%; $t(19) = 14.8$, $p < .001$). The distributions of the scores are depicted in Figure 1. Apparent are two nonoverlapping distributions, whereby the range within the AP group was wider. NAP participants did not score better than chance level (8.3%, $t(9) = 14.8$, $p = .943$).

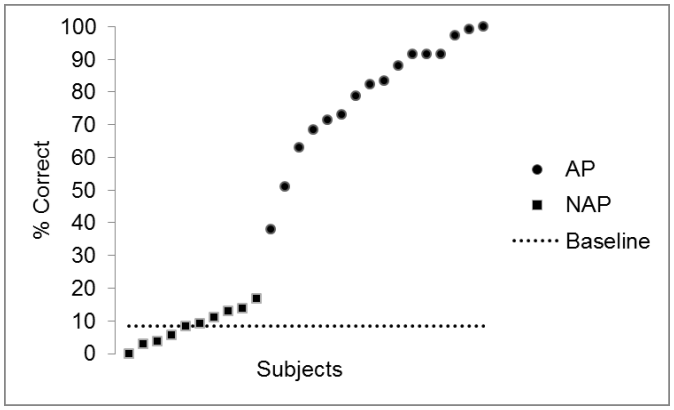

Figure 1. AP performance for each participant and the two groups.

2.2.4.2 Electrophysiological data

2.2.4.2.1 MMN and P3a

In both groups, MMN and P3a responses were elicited in all deviation conditions. For each MMN waveform, saliently inversed polarity was observed at the mastoid electrodes within the expected TW of about 100–250 msec. The P3a responses showed positive-going amplitudes at the expected TW of about 200–350 msec. Furthermore, the positive voltage distributions over the scalps were in accordance with the typical P3a scalp topography. However, spatiotemporal pattern was less pronounced in the small deviation conditions. One-sample *t*-tests revealed that all MMN and P3a amplitudes differed highly significantly from 0, which statistically justified their presences. Figures 2 and 3 illustrate the grand-averaged difference curves of all deviation conditions and both groups. The related scalp maps of the MMN and P3a responses are shown in Figure 4.

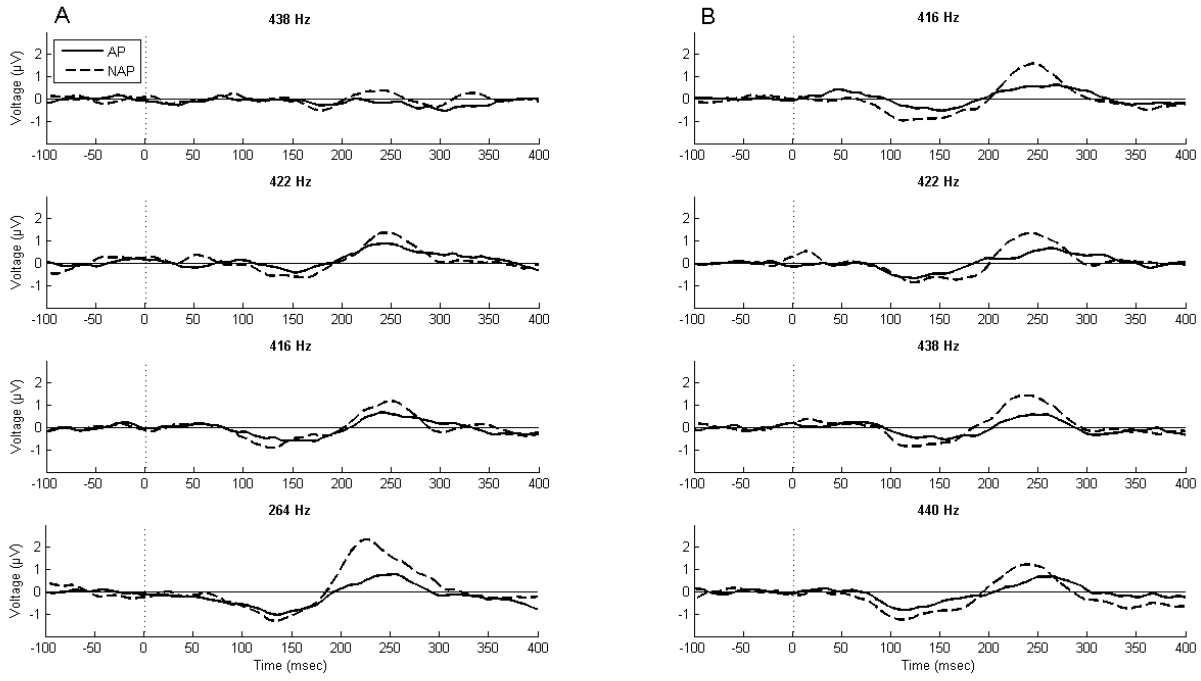

Figure 2. Grand averages of the difference waves at the frontal pool of electrodes depicted individually for each group and deviation condition (A = block A, B = block C).

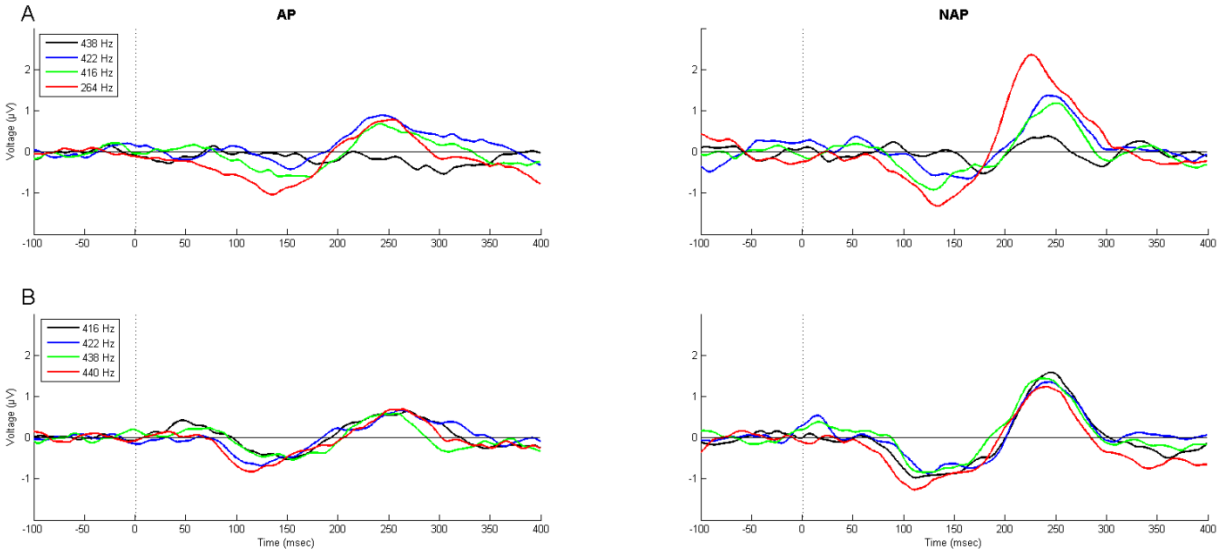

Figure 3. Grand averages of the difference waves at the frontal pool of electrodes depicted individually within each group (A = block A, B = block C).

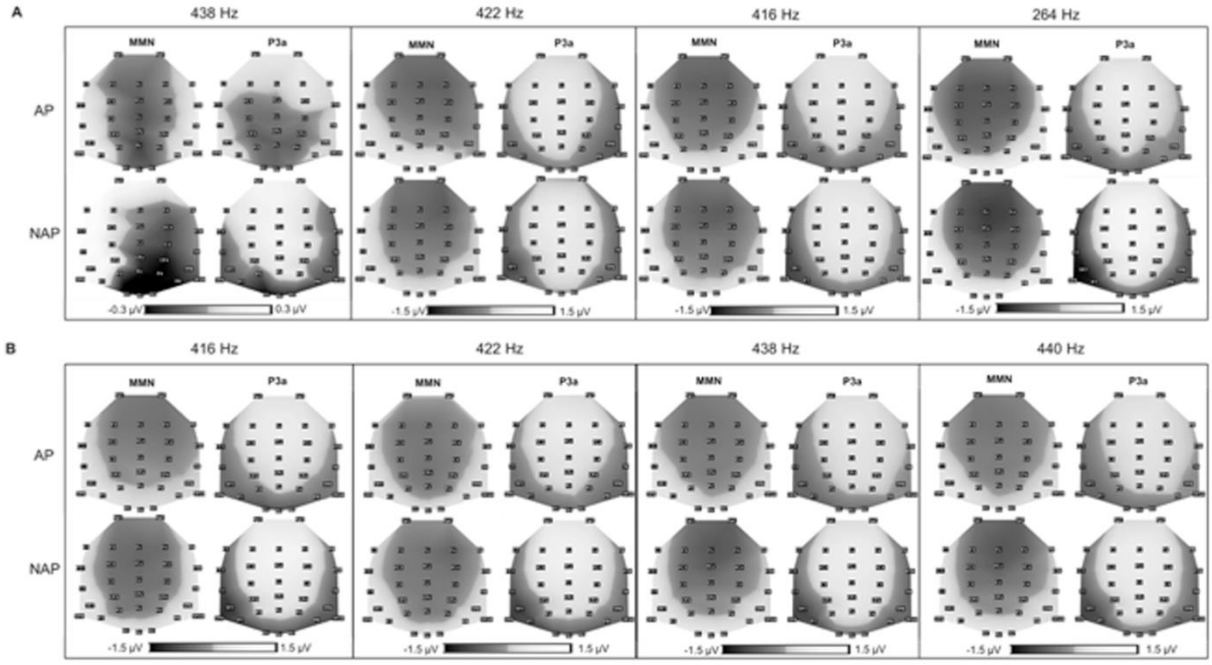

Figure 4. Scalp maps of the voltage distributions reflecting the MMN and P3a components for each group and deviation condition (A = block A, B = block C).

2.2.4.2.2 Effects of group, deviation, and interaction

Concerning the MMN amplitudes, the ANOVA calculations revealed an effect of Deviation, however, only in block A ($F(1, 24) = 10.9$, $p = .003$, $\eta p^2 = .314$; block C: $F(1, 24) = 0.92$, $p = .348$; $\eta p^2 = .037$). Otherwise, no Group differences (block A: $F(1,$

24) = 1.77, p = .195, ηp^2 = .069; block C: F(1, 24) = 3.5, p = .073, ηp^2 = .128) nor interaction effects (block A: F(1, 24) = 0.42, p = .524, ηp^2 = .017; block C: F(1, 24) = 0.014, p = .908, ηp^2 = .001) were found. Similarly, the MMN latencies showed an effect of Deviation, however, only in block A (F(1, 24) = 5.87, p = .023, ηp^2 = .196; block C: F(1, 24) = 0.018, p = .895, ηp^2 = .001). The MMN latencies showed no Group differences (Block A: F(1, 24) = 1.78, p = .195, ηp^2 = .069; block C: F(1, 24) = 2.05, p = .165, ηp^2 = .079) nor interaction effects (block A: F(1, 24) = 0.010, p = .920, ηp^2 < .001; block C: F(1, 24) = 0.031, p = .863, ηp^2 = .001). MMN amplitudes and latencies are depicted in Figure 5.

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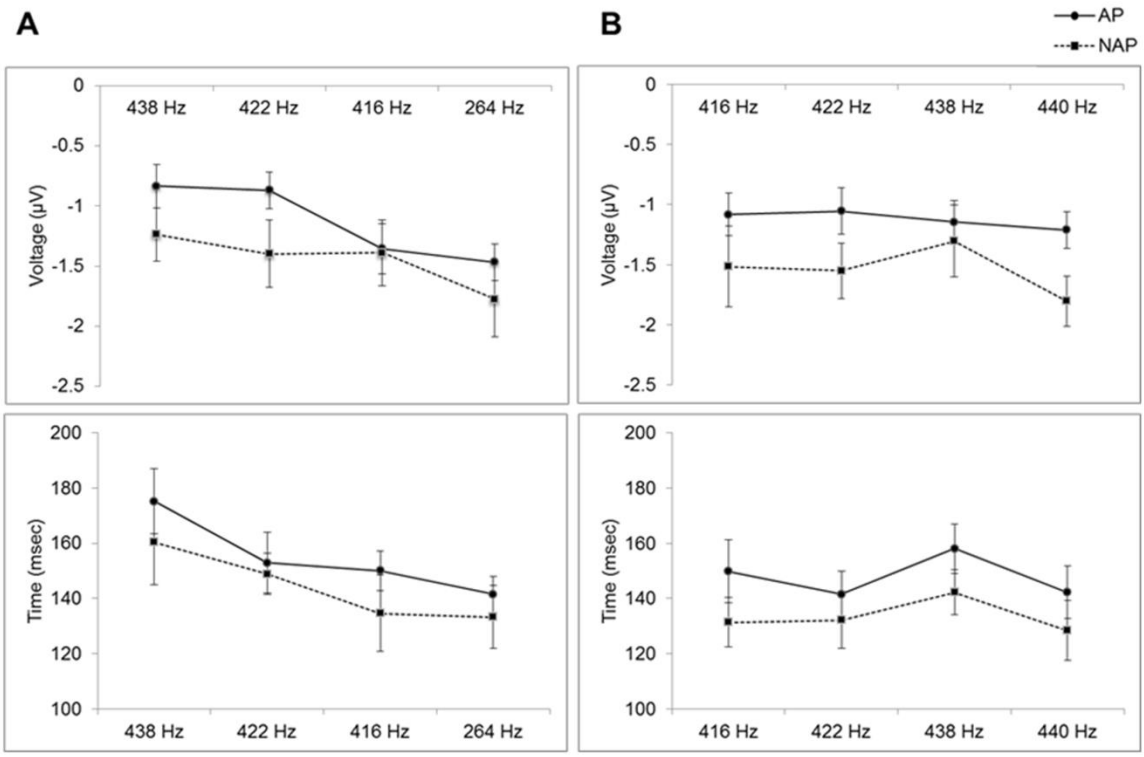

Figure 5. Amplitudes (top) and latencies (bottom) of the MMN components broken down for both groups and all deviation conditions (A = block A, B = block C). The bars depict SEMs

Concerning the P3a responses in block C, the AP participants exhibited overall significantly smaller amplitudes than the ones exhibited by NAP participants (F(1, 24) = 6.87, p = .015, ηp^2 = .223). No further Deviation (F(1, 24) = 0.305, p = .586, ηp^2 = .013) nor interaction effect (F(1, 24) = 0.312, p = .582, ηp^2 = .013) was found in this block. In block A, however, a Group difference (F(1, 24) = 10.0, p = .004, ηp^2 = .294), an effect of Deviation (F(1, 24) = 33.8, p < .001, ηp^2 = .585), and an

interaction between Group and Deviation ($F(1, 24) = 9.02$, $p = .006$, $\eta p^2 = .273$) were revealed. To further explore the interaction effect in block A, we compared the P3a amplitudes of the two groups across the four deviation conditions by performing *t*-tests for independent samples. These post hoc *t*-tests revealed a significant between-group difference in the 264 Hz condition ($t(24) = -4.62$, $p < .001$, Bonferroni-corrected $\alpha' < .05/4 = .0125$). In summary, NAP participants exhibited larger P3a amplitudes, particularly in response to between-tone category deviations (see Figure 6).

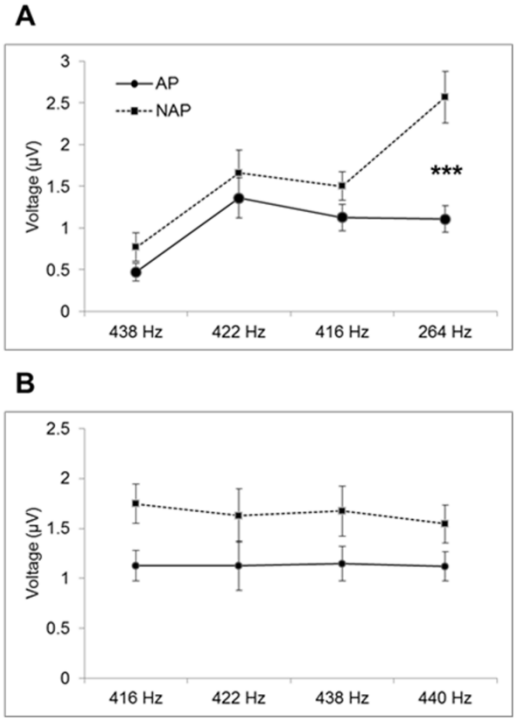

Figure 6. Amplitudes of the P3a component for both groups and all deviation conditions (A = block A, B = block C). The bars depict SEs. The asterisks indicate significant effects (***$p < .001$).

2.2.4.2.3 Correlation analyses

Correlation analyses revealed systematic relationships between the age of onset of musical training and the P3a amplitudes, however, only within the AP group. Significant positive correlations were only found in conditions with mistuned deviant tones in block A (438 Hz: r = .53, p = .017; 422 Hz: r = .54, p = .016; 416Hz: r = −.32, p = .115; 264 Hz: r = −.15, p = .295) and in block C (416 Hz: r = .24, p = .184; 422 Hz: r = .59, p = .008; 438 Hz: r = .51, p = .021; 440 Hz: r = −.15, p = .291). Within the

NAP sample no significant correlations were found between the age of onset of musical training and the P3a amplitudes neither in block A (438 Hz: r = .30, p = .201; 422 Hz: r=.32, p=.181; 416 Hz: r=−.15, p=.340; 264 Hz: r = −.4, p = .124) nor in block C (416 Hz: r = −.50, p = .069; 422 Hz: r=−.33, p=.178; 438 Hz: r=−.49, p=.074; 440 Hz: r = −.45, p = .094). All correlations are depicted in Figure 7.

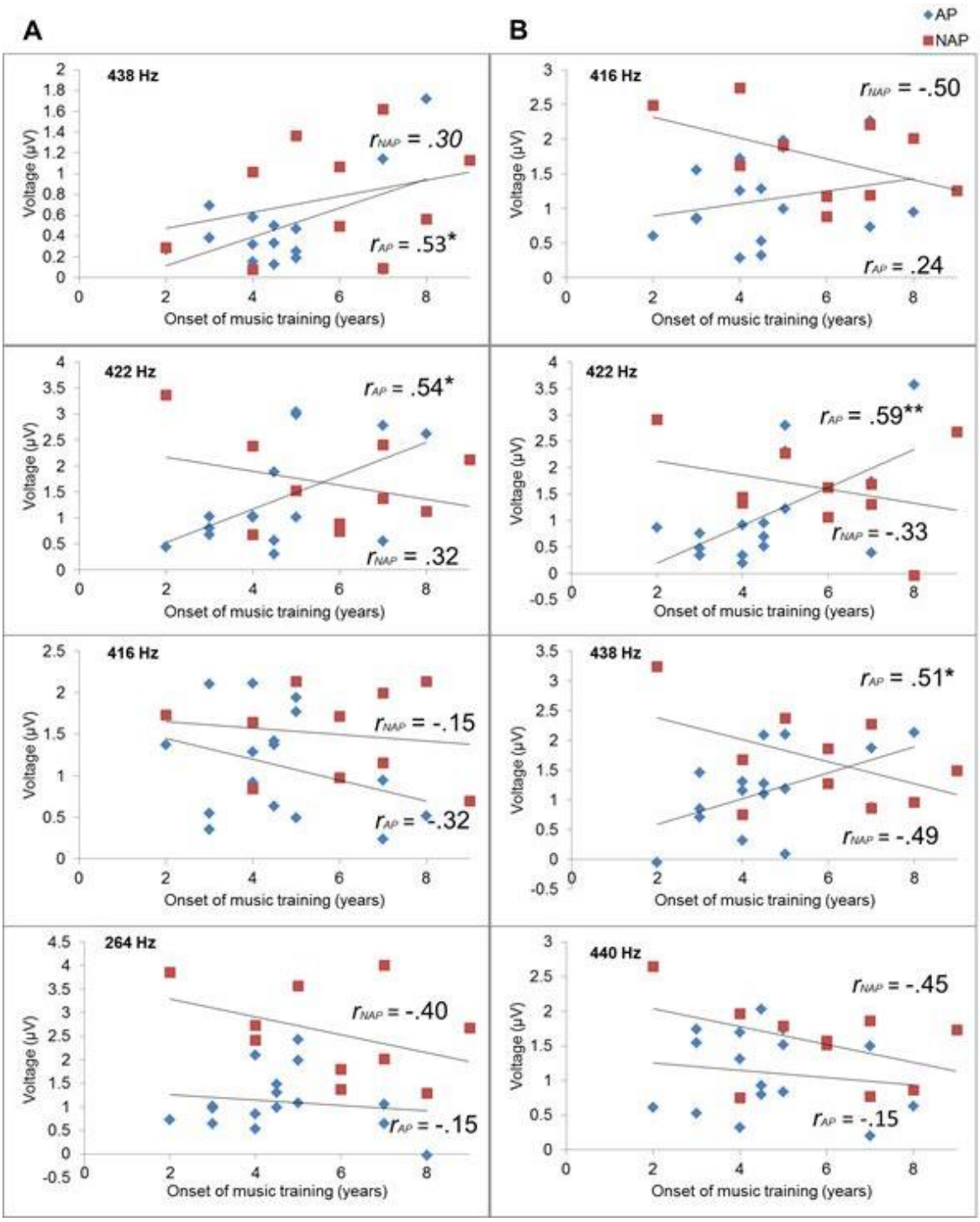

Figure 7. Correlations between age of onset of music training and the P3a amplitudes among both groups and for each deviation condition (A = block A, B = block C). The asterisks indicate the level of significant threshold (*p < .05, **p < .01).

2.2.5 Discussion

2.2.5.1 General Discussion

In the present work, we used a passive oddball paradigm for assessing the contribution of the two different processing stages to AP during passive listening. In particular, we measured the two subsequent processing stages of tone processing (i.e., early stage of auditory processing and later cognitive processing as indicated by the MMN and P3a responses, respectively) in AP and NAP participants by exploiting the excellent time resolution of the EEG technique. A first innovative aspect of our work is that we used a multiple-deviant paradigm that enables to investigate tone processing under multiple conditions (i.e., within- and between-tone categories) and degrees of deviation. A further novelty of this study is that we minimized the potential influence of top–down mechanisms, leading to the opportunity to capture the genuine and automatic features of AP (Näätänen et al., 2007; Pulvermüller & Shtyrov, 2006). Finally, in contrast to previous oddball studies (Matsuda et al., 2013; Meyer et al., 2011; Tervaniemi et al., 1993), here we controlled for the influence of physical stimulus attributes, so that both the deviant and the standard tones elicited equal frequency specific brain responses. We consider this an important point, because it has been shown that AP participants do not process pitch types equally, especially when tones are out of tune (Levitin & Rogers, 2005; Miyazaki, 1988).

In line with our hypotheses, we did not find evidence from MMN responses supporting the view that AP is related to an early pitch memory mechanism at the processing level of the auditory-related cortex. By contrast, our results confirm the specificity of the second processing stage for AP, namely, an underlying cognitive mechanism, as reflected by reduced P3a responses in AP participants. Notably, P3a responses also significantly correlated with the age of commencement of musical training, confirming the influence of early musical exposure on the ability of AP. A further innovative aspect of our work is that we are, to the best of our knowledge, the first to study the P3a component in the context of AP processing. This specific measurement is particularly fruitful in that it permits to give access to the purest and initial allocative and cognitive mechanism that is less contaminated by the influence of hierarchically higher cognitive processes, which are, for instance, likewise engaged in RP performance (see Hirose et al., 2002). In turn, we will place the

results of this study in a broader context by integrating biographical and electrophysiological data.

2.2.5.2 MMN Responses

The MMN component reflects auditory preattentive processing, operates at the sensory memory level (Garrido et al., 2009; Picton et al., 2000), but is also influenced by long-term memory (Pulvermüller & Shtyrov, 2006). Thus, this specific ERP reflects the ability to perform automatic, preattentive comparisons between successive stimuli and is considered to be an index for sound discrimination accuracy (Novak, Ritter, Vaughan, & Wiznitzer, 1990). According to a great body of studies, MMN amplitudes are known to get larger (and latencies shorter) with increased deviation level (Novitski, Tervaniemi, Huotilainen, & Näätänen, 2004; Amenedo & Escera, 2000; Sams, Paavilainen, Alho, & Näätänen, 1985).

Our MMN results, at least in block A, are fully in line with the expectation of increased amplitudes and shorter latencies as functions of increased deviation levels. In block C, however, we did not reveal such an effect of deviation. This lack of amplitude and latency modulation can easily be explained by the fact that all deviation levels reflected extreme conditions, in which the least pronounced deviation level (264 Hz vs. 416 Hz) was of eight semitones, probably leading to a salient detection effect. In line with the work of Tervaniemi et al. (1993), we did not reveal between-group differences in terms of MMN amplitudes and latencies in block A nor in block C. On the basis of these findings, we infer that AP is not necessarily driven by a differential pitch encoding ability at the processing level of the auditory-related cortex. By contrast, we propose that AP ability is more likely dependent on the second processing stage, namely the later cognitive process related to pitch labeling. Our results are further supported by a previous EEG study by Elmer et al. (Elmer, Hänggi, et al., 2013; Elmer, Sollberger, et al., 2013), which also did not reveal any differences with respect to neurophysiological processes indicating early sensory processing between AP and NAP musicians during passive listening. Certainly, we are fully aware that other authors (Matsuda et al., 2013; Schulze et al., 2013; Wu et al., 2008; Itoh et al., 2005; Ohnishi et al., 2001; Hirata et al., 1999) found evidence for auditory processing differences as a function of AP ability. However, Ohnishi et al. (2001) as well as Schulze et al. (2013) used the fMRI technique, a procedure that is

very loud and might contaminate brain responses in the auditory cortex, making it nearly impossible to disentangle whether the BOLD responses are due to scanner noise or experimental stimuli. In addition, the hemodynamic response to the auditory stimulus is too slow to disentangle the different processes on a millisecond basis, which are involved in processing the auditory information. Furthermore, in the EEG study of Hirata et al. (1999), the authors compared AP musicians with nonmusicians, without controlling for musicianship. Therefore, results are possibly more likely driven by musical practice than by AP per se. In addition, the study of Itoh et al. (2005) is not directly in contrast with our work. In fact, the authors identified an early left posterior temporal negativity, which was only present in AP participants at about 150 msec after tone presentation during tone listening and pitch-naming tasks. However, this specific deflection has been identified using scalp electrodes, which does not necessarily lead to the interpretation that the neural sources are located underneath the surface electrodes. Wu et al. (2008) were able to identify N1 effects, however, only in an active labeling task. Finally, Matsuda et al. (2013) reported larger MMN amplitudes in AP participants in response to mistuned tones but did not control for the physical attributes of the stimuli.

2.2.5.3 P3a Responses

Notably, in line with our predictions, the P3a component turned out to be a specific marker for AP. Likewise the MMN, the P3a response is driven by the magnitude of deviation (Berti, Roeber, & Schröger, 2004). However, pertaining to our data, this was only the case in block A. The lack of P3a amplitude modulation in block C was probably driven by the saliency of the deviant stimuli (see the previous section concerning the MMN). Besides this aspect, of noticeable relevance is that participants with AP exhibited overall smaller P3a amplitudes than participants without AP. This specific result suggests that tone processing in AP participants may rely on a different allocation of cognitive processes. This perspective is consistent with a large number of previous AP studies that adopted overt paradigms and reported reduced or even absent P300 amplitudes in AP participants (Crummer et al., 1994; Hantz et al., 1992; Wayman et al., 1992; Klein et al., 1984). Further evidence for the involvement of cognitive mechanisms in AP participants arises from labeling tasks, as manifested by a reduction in the P3b component, a reduction in the

posterior positive and anterior negative slow waves (Itoh et al., 2005), or by increased N400 and LPC responses (Elmer, Sollberger, et al., 2013). Overall, the reduced P3a amplitudes in our study can be explained as decreased susceptibility among AP participants responding to tones, suggesting more efficient and parsimonious cognitive processing (Bendixen et al., 2010; Wetzel & Schröger, 2007; Wetzel, Widmann, Berti, & Schröger, 2006; Berti et al., 2004; Roeber, Berti, & Schröger, 2003; Gumenyuk et al., 2001; Escera, Alho, Winkler, & Näätänen, 1998; Schröger & Wolff, 1998).

Interestingly, we also revealed a Group × Deviation level interaction effect. In block A AP participants exhibited reduced P3a responses, which were modulated as a function of deviation level. In other words, AP participants additionally differed from NAP participants, depending on whether the heard deviant tones appertained to the same tone category as the standard tone (within-tone category conditions) or corresponded to novel tone categories (between-tone category conditions). Thus, AP participants responded with even less susceptibility to such tones, gaining inefficiency. This perspective is supported by a previous behavioral study showing that AP participants react faster and more accurately when identifying musical intervals in conditions with whole tone categories (Miyazaki, 1992).

Indeed, the post hoc comparisons within block A only revealed a significant difference at the 264-Hz level (not at the 416-Hz level corresponding to A-flat). However, we still consider our line of argumentation as convincing because of the unambiguous group difference we revealed in block C comprising only between-tone category conditions. The lack of significant group difference at the 416-Hz level in block A is possibly due to a context effect. In fact, recent findings have shown that the context (e.g., chords) strongly influences tone processing (McLachlan et al., 2013). In block A, the majority of the deviant tones were narrowly spread around the standard tone, which might have had an interfering effect on processing categorical borderlines.

Taken together, our findings suggest that AP participants engage less cognitive resources while processing whole tone categories. These tones refer to the semitones used in Western music, to which one is frequently exposed to. Therefore, our interpretation is compatible with a notion established in cognitive psychology, namely that exposure frequency increases perceptual fluency and thus facilitates information processing (Bornstein & D'Agostino, 1994).

2.2.5.4 The influence of early musical training on AP

AP is assumed to develop within a sensitive period during childhood in which pitch label associations are formed (Gervain et al., 2013; Russo et al., 2003; Miyazaki, 1988). Given that during this early maturational stage the brain exhibits a high degree of plasticity (Schlaug, 2001), optimal conditions for developmental potentials are given. In connection with the impact of the sensitive period on AP acquisition, a large number of studies also reported benefits in starting earlier with musical training (Deutsch et al., 2006; Gregersen et al., 2001), as reflected by neurophysiological and neuroanatomical correlates (Meyer et al., 2011; Imfeld, Oechslin, Meyer, Loenneker, & Jancke, 2009; Ohnishi et al., 2001). In line with this perspective, we revealed positive correlations between the age of commencement of musical training and P3a amplitudes, meaning that AP participants who started earlier with musical training were characterized by reduced P3a amplitudes. However, this relationship was only found in conditions in which the deviant tones were mistuned, indicating that the later the AP participants started with music training, the larger the P3a amplitudes peaked in response to tones that are not considered as being part of the Western musical system. Therefore, we may speculate whether early training commencement may facilitate more demanding pitch processing. Finally, the question arises here whether transfer effects between the processing of tones from the Western musical system and the processing of tones from not acquired tonal systems are modulated by the exposure to musical training during early childhood.

2.2.5.5 Multiple codes and pitch-labeling performance

AP ability has been suggested to be dependent on mental codes, which are supposed to facilitate labeling performance (Zatorre et al., 1998; Zatorre & Beckett, 1989). Evidence in this direction arises from previous work, indicating decreased working memory loads (reduced P300 responses) in AP participants while counting auditory oddballs (Hantz et al., 1992; Klein et al., 1984). Furthermore, there is evidence showing that blocking verbal rehearsal in AP participants does not seem to affect tone label retention (Zatorre & Beckett, 1989), this suggesting that multiple

codes (verbal, auditory imagery, sensorimotor cues) are involved in AP (Zatorre, 2003; Zatorre et al., 1998; Zatorre & Beckett, 1989). Taken together, these previous results suggest that AP underlies multimodal processes that are dependent on associative brain areas (Zatorre et al., 1998).

On the basis of a vast body of evidence suggesting that multimodal processing has facilitatory effects on task performance (Shams & Seitz, 2008; Fort, Delpuech, Pernier, & Giard, 2002; Giard & Peronnet, 1999), we argue that the reduced P3a amplitudes we revealed in AP participants are possibly related to the availability of multiple codes, enabling a more efficient allocation of attentional functions. In fact, it appears plausible to assume that the pitch types, which have explicitly been acquired in the coding process during the sensitive period, are more efficiently processed. Possibly, the reduction of the P3a responses in this context reflects the establishment of cognitive resources on which pitch labeling relies, because reduced P3a responses have repeatedly been associated with more efficient cognitive and behavioral performance (Bendixen et al., 2010; Wetzel & Schröger, 2007; Wetzel et al., 2006; Berti et al., 2004; Roeber et al., 2003; Gumenyuk et al., 2001; Escera et al., 1998; Schröger & Wolff, 1998).

2.2.5.6 Conclusion

By means of a passive oddball paradigm, we provide first evidence showing that even in a passive listening condition rather a cognitive than a sensory mechanism contributes to the phenomenon of AP. The reduction in the P3a responses we revealed in AP participants reflects a more efficient and parsimonious allocation of cognitive demands because of a multidimensional tone processing. Efficiency appears to depend on the extent of experience in processing pitches during the sensitive period. Our findings are in line with the growing consensus (Elmer, Hänggi, et al., 2013; Elmer, Sollberger, et al., 2013; Levitin & Rogers, 2005; Zatorre et al., 1998; Levitin, 1994) considering the later-occurring and cognitively based processing stage as the crucial operation for AP.

2.2.6 Acknowledgments

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2.3 Study 2: Independent component processes underlying emotions during natural music listening

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2.3.1 Abstract

The aim of this study was to investigate the brain processes underlying emotions during natural music listening. To address this, we recorded high-density electroencephalography (EEG) from 22 subjects while presenting a set of individually matched whole musical excerpts varying in valence and arousal. Independent component analysis was applied to decompose the EEG data into functionally distinct brain processes. A k-means cluster analysis calculated on the basis of a combination of spatial (scalp topography and dipole location mapped onto the Montreal Neurological Institute brain template) and functional (spectra) characteristics revealed 10 clusters referring to brain areas typically involved in music and emotion processing, namely in the proximity of thalamic-limbic and orbitofrontal regions as well as at frontal, fronto-parietal, parietal, parieto-occipital, temporo-occipital and occipital areas. This analysis revealed that arousal was associated with a suppression of power in the alpha frequency range. On the other hand, valence was associated with an increase in theta frequency power in response to excerpts inducing happiness compared to sadness. These findings are partly compatible with the model proposed by Heller, arguing that the frontal lobe is involved in modulating valenced experiences (the left frontal hemisphere for positive emotions) whereas the right parieto-temporal region contributes to the emotional arousal.

2.3.2 Introduction

A considerable part of our everyday emotions is due to music listening (Juslin et al., 2008). Music, a cultural universal, serves social functions (Juslin and Laukka, 2003; Hagen and Bryant, 2003), and has the power to evoke emotions and influence moods (Goldstein, 1980; Sloboda, 1991; Sloboda et al., 2001; Baumgartner et al., 2006a,b). In fact, regulating these affective states is our main motivation for engaging with music (Panksepp, 1995; Juslin and Laukka, 2004; Thoma et al., 2011a,b). Affective research already provided many valuable insights into the underlying mechanisms of music-evoked emotions. For example, there is consensus that specific limbic (e.g. nucleus accumbens and amygdala), paralimbic (e.g. insular and orbitofrontal cortex) and neocortical brain areas (e.g. fronto-temporal-parietal areas) contribute to music-evoked emotions that partly also underlie non-musical emotional

experiences in everyday life (Blood et al., 1999; Koelsch, 2014). Pleasure experienced during music listening is associated with mesolimbic–striatal structures (Blood et al., 1999; Blood and Zatorre, 2001; Brown et al., 2004; Menon and Levitin, 2005; Salimpoor et al., 2011, 2013) also involved in experiencing pleasure in various reward-related behaviors such as sex (Pfaus et al., 1995; Aron et al., 2005; Komisaruk and Whipple, 2005), feeding (Hernandez and Hoebel, 1988; Berridge, 2003; Small et al., 2003) or even money handling (Knutson et al., 2001). In contrast, the amygdala (another limbic core structure) is mostly associated with negatively valenced emotions experienced during music listening (Koelsch et al., 2006; Mitterschiffthaler et al., 2007; Koelsch et al., 2008) as well as in response to a wide range of non-musical aversive stimuli (Phan et al., 2002). However, these phylogenetically old circuits interact with neocortical areas (Zatorre et al., 2007; Salimpoor et al., 2013; Zatorre and Salimpoor, 2013), enabling the emergence of more complex and music-specific (so-called 'aesthetic'; Scherer, 2004) emotions, such as the ones classified by the Geneva Emotional Music Scale (GEMS) (Zentner et al., 2008; Brattico and Jacobsen, 2009; Trost et al., 2012). Further agreement among researchers concerns the hemispheric lateralization of functions related to emotions, as provided by a great body of neuroimaging and clinical studies making frontal (Hughlings-Jackson, 1878; Davidson, 2004, 1998; Hagemann et al., 1998; Sutton and Davidson, 2000; Craig, 2005) or global lateralization a subject of discussion (Silberman and Weingartner, 1986; Henriques and Davidson, 1991; Meadows and Kaplan, 1994; Hagemann et al., 2003). In this context, it is important to remark that similar effects of lateralization also underlie music-evoked emotions. In fact, music-related studies using electroencephalography (EEG) have provided evidence indicating that the right frontal brain region preferably contributes to arousal and negatively valenced emotions, whereas the left one to positively valenced emotions (Schmidt and Trainor, 2001; Tsang et al., 2001; Altenmüller et al., 2002; Mikutta et al., 2012). Despite music's effectiveness in evoking emotions and its closeness to everyday life, within affective research music is not the most preferred stimulus material. To a certain extent, this restraint is due to the idiosyncratic nature of musical experiences (Gowensmith and Bloom, 1997; Juslin and Laukka, 2004; Zatorre, 2005). Otherwise, there is evidence indicating a certain stability of music-evoked emotional experiences across cultures (Peretz and Hebert, 2000; Trehub, 2003) in response to specific elementary musical structures such as the musical

mode (major/minor) and tempo inducing happiness and sadness (Hevner, 1935, 1937; Peretz et al., 1998; Dalla Bella et al., 2001), or consonant (dissonant) music intervals inducing (un)pleasantness (Bigand et al., 1996; Trainor and Heinmiller, 1998; Zentner and Kagan, 1998). However, these physical features possess only negligible explanatory power considering the full variability of musical experiences among humans. Another crucial problem here refers to the fact that authentic music-evoked emotions unfold particularly over time (Koelsch et al., 2006; Sammler et al., 2007; Bachorik et al., 2009; Lehne et al., 2013; Jancke et al., 2015), as for example due to violation or confirmation of established expectancies (Meyer, 1956; Sloboda, 1991). Temporal characteristics and specific moments accounting for music-evoked emotions are not only reflected behaviorally (Grewe et al., 2007; Bachorik et al., 2009), but also in psychophysiological activity (Grewe et al., 2005; Grewe et al., 2007; Lundqvist et al., 2008; Grewe et al., 2009; Koelsch and Jancke, 2015), and in brain activity (Koelsch et al., 2006; Lehne et al., 2013; Trost et al., 2015). Such temporal dynamics of emotional experiences requires rather longer stimuli for experimental purposes, challenging research implementation especially in terms of classical event-related paradigms. Thus, alternative methods are indicated to more fully capture music-evoked emotions.

Independent component analysis (ICA) is a promising data driven approach increasingly used to investigate brain states during real-world experiences. From complex brain activities, ICA allows to ‘blindly’ determine distinct neural sources with independent time courses associated with features of interest while ensuring an optimal signal-to-noise ratio (Jutten and Herault, 1991; Makeig et al., 1996; Makeig et al., 1997; Makeig et al., 2000; Jung et al., 2001; Makeig et al., 2004; Lemm et al., 2006). So far, ICA has already been proved to be fruitful in gaining insights into natural music processing (Schmithorst, 2005; Sridharan et al., 2007; Lin et al., 2010; Cong et al., 2013; Cong et al., 2014; Lin et al., 2014), but additionally in other real-world conditions such as resting state (Damoiseaux et al., 2006; Mantini et al., 2007; Jancke and Alahmadi, 2015), natural film watching (Bartels and Zeki, 2004, 2005; Malinen et al., 2007) and the riddle of the cocktail party effect (Bell and Sejnowski, 1995).

By applying ICA in combination with high-density EEG, this study aims at examining the independent components (IC) underlying music-evoked emotions. In particular, this study attempts to provide an ecologically valid prerequisite for natural

music listening by including whole music excerpts with sufficient length as experimental stimuli. Similar to previous music-related studies (Schubert, 1999; Schmidt and Trainor, 2001; Chapin et al., 2010; Lin et al., 2010), we analyzed music-evoked emotions in terms of two affective dimensions, namely scales representing valence and arousal. We manipulated musical experience by presenting different musical excerpts corresponding to different manifestations on these two dimensions. Subject-wise, we provided individual sets of stimuli in order to take into consideration the idiosyncratic nature of musical experiences. Despite the exposure of non-identical stimuli across subjects, we expected ICA to reveal functionally distinct EEG sources contributing to the both affective dimensions.

2.3.3 Materials and methods

2.3.3.1 Participants

Twenty-two subjects (13 female, age range 19–30 years, 110 M = 24.2, s.d. = 3.1) who generally enjoyed listening to music but were not actively engaged in making music for at least the past 5 years participated in this study; 29.4% of the subjects had never played a musical instrument. According to the Advanced Measures of Music Audition test (Gordon, 1989), the subjects ranked on average on the 56th percentile, indicating a musical aptitude corresponding to 56% of the non-musical population. At the time of the study as well as for the last 10 years, the subjects listened to music of various genres between 1 and 3 h per day. According to the Annett-Handedness-Questionnaire (Annett, 1970), all participants were consistently right-handed. Participants gave written consent in accordance with the Declaration of Helsinki and procedures approved by the local ethics committee and were paid for participation. None of the participants had any history of neurological, psychiatric or audiological disorders.

2.3.3.2 Stimuli

A pool of 40 various musical excerpts was heuristically assembled by psychology students from our lab with the aim of equally covering each quadrant of

the two-dimensional affective space. The musical excerpts were of different genres namely of soundtracks, classical music, ballet and operas but did not contain any vocals. The pool of musical excerpts is listed in Table 1.

Table 1 Musical excerpts

Composer	Excerpt	Neg	Pos	High	Low
Albinoni, T.	Adagio, G Minor (7'40)	.64	0	.27	.36
Alfvén, H.	Midsommarvaka (0'02)	0	.55	.36	.18
Barber, S.	Adagio for Strings (1’00)	.64	.05	.45	.23
Barber, S.	Adagio for Strings (5’10)	.41	0	.32	.09
Beethoven, L.	Symphony No. 6 "Pastoral" 3rd Mvt. (2’30)	0	.77	.68	.09
Beethoven, L.	Moonlight Sonata, 1st Mvt. (0’19)	.77	0	.41	.36
Boccherini, L.	Minuetto (0’00)	0	.5	.36	.14
Chopin, F.	Mazurka Op 7 No. 1, B flat Major (0’00)	0	.5	.14	.41
Corelli, A.	Christmas Concerto - Vivace-Grave (0’20)	.55	0	.09	.45
Galuppi, B.	Sonata No. 5, C Major (0’00)	0	.32	0	.32
Grieg, E.	Suite No. 1, Op. 46 - Aase's Death (1’22)	.68	.05	.36	.36
Händel, GF.	Water Music, Suite No. 2 D Major Alla Hornpipe (0’00)	0	.68	.45	.23
Haydn, J.	Andante Cantabile from String Quartet Op. 3 No. 5 (0’00)	.09	.32	.09	.32
Mozart, A.	Clarinet Concerto, A Major, K 622 Adagio (0’00)	.09	.32	.19	.23
Mozart, A.	Eine kleine Nachtmusik – Allegro (2’04)	0	.73	.59	.14
Mozart, A.	Eine kleine Nachtmusik – Rondo allegro (0’00)	0	.5	.32	.19
Mozart, A.	Manuetto, Trio, KV 68 (0’00)	0	.36	0	.36
Mozart, A.	Piano Sonata No. 10, C Major, K. 330 – Allegro moderato (0’00)	0	.5	.18	.36
Mozart, A.	Rondo, D Major, K. 485 (0’00)	0	.59	.19	.4
Mozart, A.	Violin Concerto No. 3, G Major, K. 216 1st Mvt. (0’00)	0	.5	.27	.23
Murphy, J.	Sunshine – Adagio, D Minor (1’30)	.32	.27	.55	.05
Murphy, J.	28 days later - Theme Soundtrack (0’25)	.64	.05	.41	.27
Ortega, M.	It's hard to say goodbye (0’00)	.45	0	.27	.18
Pyeong Keyon, J.	Sad romance (0’00)	.77	0	.59	.18
Rodriguez, R.	Once upon a time in Mexico – Main Theme (0’00)	.45	.05	.18	.32
Rossini, G.	Die diebische Elster (la gazza ladra), Ouvertüre (3'47)	0	.45	.27	.18
Scarlatti, D.	Sonata, E Major, K. 380 – Andante comodo (0’30)	0	.55	0	.55
Schumann, R.	Kinderszenen – Von fremden Ländern und Menschen (0’00)	.05	.36	.05	.36
Shostakovich, D.	Prelude for Violin and Piano (0’00)	.68	0	.41	.27
Strauss, J.	Pizzicato Polka (0’00)	0	.5	.36	.14
Tiersen, Y.	I saw daddy today, Goodbye Lenin (0'25)	.86	0	.32	.55
Tiersen, Y.	Sur le fil, Amélie (1'40)	.55	0	.05	.5
Tschaikowsky, P.	Danse Espagnole (0’20)	0	.59	.45	.14
Vagabond	One hour before the trip (1'39)	.14	0	.05	.09
Vivaldi, A.	Concerto, A Major, p. 235, Allegro (0’00)	0	.59	.41	.18
Vivaldi, A.	Concerto for 2 violins, D major RV 512	.45	.05	.05	.45

	(1'15)				
Vivaldi, A.	Spring: II. Largo (0’00)	.73	0	.23	.5
Webber, JLP.	Return to paradise (0’05)	.64	0	.45	.18
Chowhan, P. Yiruma	Kiss The Rain, Twilight (0’00)	.45	.05	.18	.32
Zimmer, H.	This Land, Lion King (0’45)	.45	.18	.64	0

Notes: Listed are all musical excerpts with occurrence frequency for each condition. Neg, negatively valenced; Pos, positively valenced; High, highly arousing; Low, lowly arousing. Excerpt onsets are indicated in brackets

Each musical excerpt was 60 s of length, stored in MP3 format on hard disk, logarithmically smoothed with a rise and fall time of 2 s to avoid an abrupt decay, and normalized in amplitude to 100% (corresponding to 0 decibel full scale, i.e. dB FS) by using Adobe Audition 1.5 (Adobe Systems, Inc., San Jose, CA). This is an automatized process that changes the level of each sample in a digital audio signal by the same amount, such that the loudest sample reaches a specified level. Consequently, the volume was consistent throughout all musical pieces presented to the participants.

2.3.3.3 Experimental procedure

2.3.3.3.1 Online rating

Prior to the main experimental session, participants rated all 40 musical excerpts at home according to the valence and arousal dimension via open source platform called ‘Online Learning and Training’ (OLAT, provided by the University of Zurich, http://www.olat.org/). Seven-point scales were provided to assess the experienced emotions in response to each musical excerpt. The scale representing valence ranged from -3 (sad) to +3 (happy), whereas the scale representing arousal ranged from 0 (calm) to +6 (stimulating).

2.3.3.3.2 Experimental session

The sets of stimuli presented during EEG recording were assembled subject-wise based on median splits calculated for the individual online ratings so that half of the stimuli represented both opposite parts of the valence and the 5 arousal

dimension, respectively. These sets contained 24 musical excerpts, reflecting most extreme values represented within this two-dimensional affective space. Table 1 shows the occurrence of each stimulus during EEG recording. For each musical excerpt, the tempo, tonal centroid and zero-crossing rate were extracted using the Music Information Retrieval toolbox (Lartillot and Toiviainen, 2007). Regarding these values, the subject-wise selected stimuli did not differ between the conditions, indicating overall comparability in the rhythmic [valence: $t(21) = 0.996$, $P = 0.331$; arousal: $t(21) = 0.842$, $P = 0.409$], tonal [valence: $t(21) = 0.505$, $P = 0.619$; arousal: $t(21) = 1.141$, $P = 0.267$) and timbral structure [valence: $t(21) = 0.714$, $P = 0.482$; arousal: $t(21) = 1.968$, $P = 0.062$].

During EEG measurements, the participants were placed on a comfortable chair in a dimmed and acoustically shielded room, at a distance of about 100 cm from a monitor. They were instructed to sit quietly, to relax and to look at the fixation mark on the screen to minimize muscle and eye movement artifacts. All musical excerpts were delivered binaurally with a sound pressure level of about 80 dB by using HiFi headphones 25 (Sennheiser, HD 25-1, 70 X, Ireland). The participants were required to, respectively, rate their experienced emotions after listening to each musical excerpt. Ratings were performed by presenting two 5-degreed Self-Assessment Manikin (SAM) (Bradley and Lang, 1994), reflecting valence and arousal. The SAM scales contain non-verbal graphical depictions, whereby rating responses were also recorded between the depictions. The valence scale ranged from 10 to 10, whereas the arousal scale ranged from 0 to 10. After each stimulus rating, a baseline period of 30 s followed. The presentation of the stimuli and the recording of behavioral responses were controlled by the Presentation software (Neurobehavioral Systems, Albany, CA; version 17.0).

2.3.3.4 Data acquisition

The high-density EEG (128 channels) was recorded with a sampling rate of 500 Hz and a band pass filter from 0.3 to 100 Hz (Electrical Geodesics, Eugene, OR). Electrode Cz served as online reference, and impedances were kept below 30 kX. Before data pre-processing, the electrodes in the outermost circumference were removed, resulting in a standard 109-channel electrode array.

2.3.3.5 Data processing and analyses

2.3.3.5.1 Preprocessing

Raw EEG data were imported into EEGLAB v.13.2.1 (Delorme and Makeig, 2004; http://www.sccn.ucsd.edu/eeglab), an open source toolbox running under Matlab R2013b (MathWorks, Natick, MA, USA). Raw EEG data were band-pass 50 filtered at 1–100 Hz and re-referenced to an average reference. Noisy channels exceeding averaged kurtosis and probability Z-scores of 65 were removed. On average, 8.4% (s.d. = 3.4) of the channels were removed. Unsystematic artifacts were removed and reconstructed by using the Artifact Subspace Reconstruction method (Mullen et al., 2013; e.g. Jäncke et al., 2015; http://sccn.ucsd.edu/eeglab/plugins/ASR.pdf) and electrical line noise was removed by the CleanLine function (e.g. Brodie et al., 2014; http://www.nitrc.org/projects/cleanline).

For each musical excerpt, segments of 65 s duration were 60 created, including a 5 s pre-stimulus period. Furthermore, a baseline correction relative to the 5 to 0 s pre-stimulus time period was applied.

2.3.3.5.2 Independent component analysis

The epoched EEG data were decomposed into temporally maximally independent signals using the extended infomax ICA algorithm (Lee et al., 1999).

ICA determines the ‘unmixing’ matrix W with which it unmixes the multi-channel EEG data X into a matrix U comprising the channel-weighted sum of statistically IC activity time courses. Thus, U equals WX. For ICA, we used an iteration procedure based on the ‘binica’ algorithm with default parameters implemented in EEGLAB (stopping weight change = 10^{-7}, maximal 1000 learning steps) (Makeig et al., 1997), revealing as many ICs as data channels. ICs not corresponding to cortical sources such as eye blinks, lateral eye movement and cardiac artifacts were excluded from further analyses. Given that only ICs with dipolar scalp projections appear as biologically plausible brain sources (Makeig et al., 2002; Delorme et al., 2012), only such were included in further analyses. Thus for each IC,

we estimated a single-equivalent current dipole model and fitted the corresponding dipole sources within a co- registered boundary element head model (BEM) by using the FieldTrip function DIPFIT 2.2 (http://sccn.ucsd.edu/wiki/A08:_DIPFIT). Furthermore, dipole localizations were mapped to the Montreal Neurological Institute brain template. Only ICs accounting for more than 85% of variance of the best-fitting single-equivalent dipole model were further processed (Onton and Makeig, 2006).

2.3.3.5.3 Spectral analysis

A 512-point Fast Fourier transform with a 50% overlapping Hanning window of 1 s was applied to compute the IC spectrogram for each segment. The power of each segment was normalized by subtracting a mean baseline derived from 90 the first 5 s of stimulus onset (Lin et al., 2010, 2014). The spectrogram was then divided into the five characteristic frequency bands, namely delta (1–4 Hz), theta (4–7 Hz), alpha-1 (8–10.5 Hz), alpha-2 (10.5–13 Hz) and beta (14–30 Hz).

2.3.3.5.4 IC clustering

In order to capture functionally equal ICs across all participants and enable group-level analyses, we applied cluster analyses based on the k-means algorithm. All ICs from all participants were clustered on the basis of the combination of spatial (dipole location and scalp topography) as well as functional (spectra) characteristics (Onton and Makeig, 2006). The smallest exhibited number of ICs determined the number of clusters used for this calculation (Lenartowicz et al., 2014). Furthermore, we removed ICs whose centroids were 3 s.d. of Euclidean distance away from fitting into any of the other clusters (Wisniewski et al., 2012). After calculating the cluster analysis, we visually confirmed consistency of the ICs within each cluster in terms of spatial and functional characteristics.

2.3.3.5.5 Statistical analyses

Responses to all musical excerpts were analyzed regarding the valence and

arousal dimension independently from each other. The excerpt ratings during EEG recording were subject-wise and condition-wise averaged. Paired t-tests were used to statistically compare averaged responses to positively with negatively valenced excerpts as well as to highly with lowly arousing ones, respectively. In order to determine the affective effects on brain activity regarding each IC cluster, we conducted analyses of variance (ANOVA) with two repeated measurements, one with a five-way factor (delta, theta, alpha-1, alpha-2 and beta) and another one with a two-way factor (high vs low arousal or positive vs negative valence). Statistical analyses were adjusted for non-sphericity using Greenhouse–Geisser Epsilon when equal variances could not be assumed. Significant interaction effects were further inspected by using post hoc t-tests. All post hoc t-tests were corrected for multiple comparisons by using the Holm procedure (Holm, 1979).

As it is important to report the strength of an effect independent of the sample size, we also calculated the effect size (ηp^2) by dividing the sums of squares of the effects by the sums of squares of these effects plus its associated error variance within the ANOVA computation. All statistical analyses were performed using the SPSS software (SPSS 19 for Windows; www.spss.com).

2.3.4 Results

2.3.4.1 Behavioral data

As confirmed by the ratings during EEG recording, the participants experienced the musical excerpts in accordance with the conditions they were previously assembled for. Ratings between the positively valenced (M = 4.4, s.d. = 1.7) and negatively valenced stimuli (M = 4.0, s.d. = 1.7) differed significantly from each other [$t(21) = 14.2$, $P < 0.001$]. Furthermore, the participants rated highly arousing stimuli (M = 6.2, s.d. = 1.4) significantly more arousing than low arousing ones [M = 4.1, s.d. = 1.4; $t(21) = 10.7$, $P < 0.001$]. Behavioral results are depicted in Figure 1.

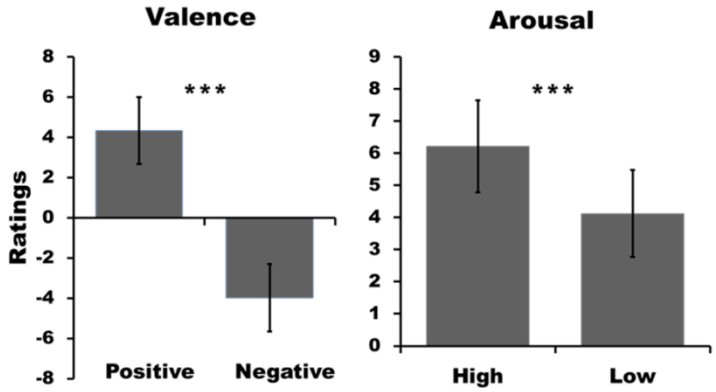

Fig. 1. Mean ratings of the stimuli during the EEG session, separately for the valence (left) and arousal (right) dimensions. The bars depict standard deviations. The asterisks indicate the level of significant threshold (***$P < 0.001$).

2.3.4.2 Electrophysiological data

2.3.4.2.1 IC clusters

Our cluster analysis on the estimated single-equivalent current dipoles fitted within the BEM using the DIPFIT function revealed 10 IC clusters. Sample size and the number of the ICs contained by each cluster, the Talairach coordinates of the particular centroids as well as the residual variances (RV) of the fitted models are reported in Table 2.

Table 2. IC clusters and the centroids of their dipole location

#	Cluster	N	ICs	x	y	z	RV%
1	Limbic-thalamic	11	16	-3 (18)	-9 (12)	10 (9)	11 (3)
2	Orbitofrontal	14	21	-10 (18)	25 (21)	-24 (6)	9 (2)
3	L frontal	11	15	-28 (21)	30 (15)	29 (12)	11 (3)
4	R frontal	11	12	19 (12)	38 (19)	32 (12)	12 (2)
5	Fronto-parietal	11	22	17 (13)	-18 (13)	52 (14)	10 (3)
6	Precuneous	15	19	0 (12)	-49 (12)	50 (13)	9 (3)
7	Parieto-occipital	17	31	-4 (14)	-75 (13)	22 (13)	11 (3)
8	R temporal-occipital	9	14	41 (18)	-49 (16)	-4 (15)	10 (3)
9	L occipital	15	22	-24 (12)	-87 (10)	-16 (10)	10 (3)
10	R occipital	17	24	13 (10)	-86 (11)	-18 (10)	10 (3)

Notes: Listed are all musical excerpts with occurrence frequency for each condition. Neg, negatively valenced; Pos, positively valenced; High, highly arousing; Low, lowly arousing. Excerpt onsets are indicated in brackets.

Two of the centroids (#1 and 2) were modeled mainly within subcortical regions, exhibiting individual dipoles located in the thalamus, amygdala,

parahippocampus, posterior cingulate and insular cortex as well as in the orbitofrontal cortex. Two of them were modeled near the frontal midline, namely left- (# 3) and right-lateralized (# 4), exhibiting dipoles distributed around the inferior, middle and superior frontal lobe. Five of them were modeled within 'junction' regions between lobes: cluster #5 covered regions from frontal (precentral gyrus, superior, middle and medial frontal gyrus) to parietal (postcentral gyrus) and around the posterior insular cortex. Cluster #6 was mainly located in the precuneus but additionally included other parietal regions (postcentral gyrus, superior parietal lobus). The individual dipoles of cluster #7 were distributed around the parietal–occipital junction (centralized around the cuneus) and cluster #8 was right-lateralized covering temporal–occipital regions (middle occipital lobe, superior-, middle- and inferior temporal lobe). Finally, the two remaining centroids were modeled within posterior regions, left- (#9) and right-lateralized (#10), exhibiting individual dipoles distributed around the occipital lobe (fusiform gyrus, lingual gyrus) and cerebellar structures. In addition, most of the clusters exhibited few individual dipoles in the anterior and posterior cingulate cortex, namely in BA 24 (#5), BA 30 (#7, 8, 9), BA 31 (#5, 6, 7) and BA 32 (#3).

Scalp topographies, dipole locations and spectra of each IC cluster are depicted in Figure 2.

2.3.4.2.2 IC spectra

No cluster reached any significant main effects of valence or arousal, but all of them revealed significant main effects of frequency ($P< 0.001$, $\eta p^2> 0.8$). Only two clusters revealed significant interaction effects. Cluster #3 exhibited a significant valence x frequency effect [$F(1,10) = 5.96$, $P =0.035$, $\eta p^2= 0.373$]. According to post hoc *t*-tests, this effect was due to theta power. Positive valence was associated with a power increase in this frequency band [$t(10) = -2.77$ $P< 0.01$]. This accounted for 24.09% of EEG variance. Cluster #10 exhibited a significant arousal frequency effect [$F(1,16) = 15.928$, $P < 0.001$, $\eta p^2> 0.499$]. This effect was due to alpha-2 activity. Arousal was associated with a power suppression in this frequency band [$t(16)= -2.133$ $P= 0.025$]. This accounted for 34.85% of EEG variance.

Figure 3 illustrates these two interaction effects in terms of differences calculated between the two affective conditions.

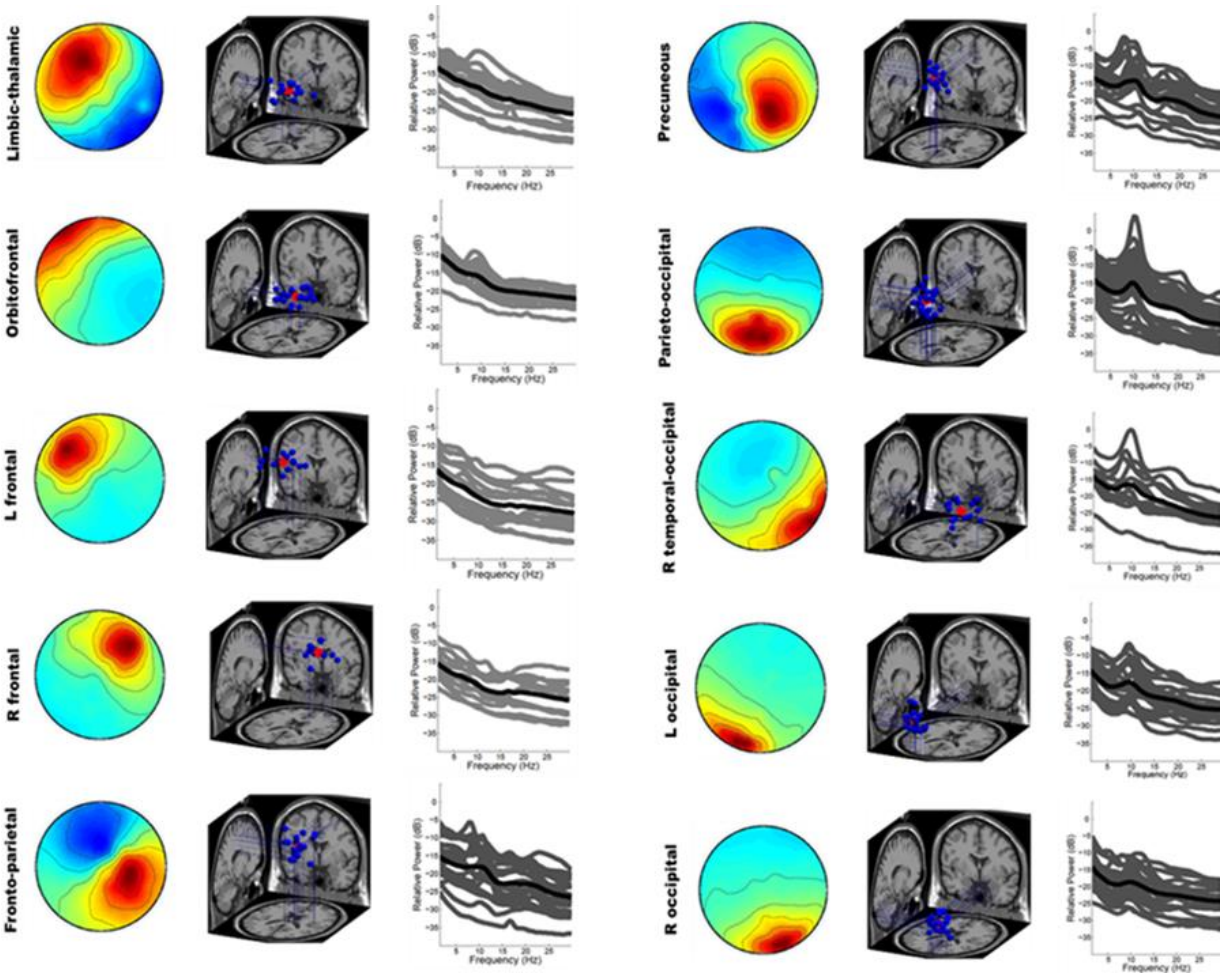

Fig. 2. IC clusters: mean scalp maps showing distribution of relative projection strengths (W^{-1}; warm colors indicating positive and cold colors negative values); dipole source locations (red = centroid; blue = individual dipoles) and spectrogram (black = mean; gray = individual).

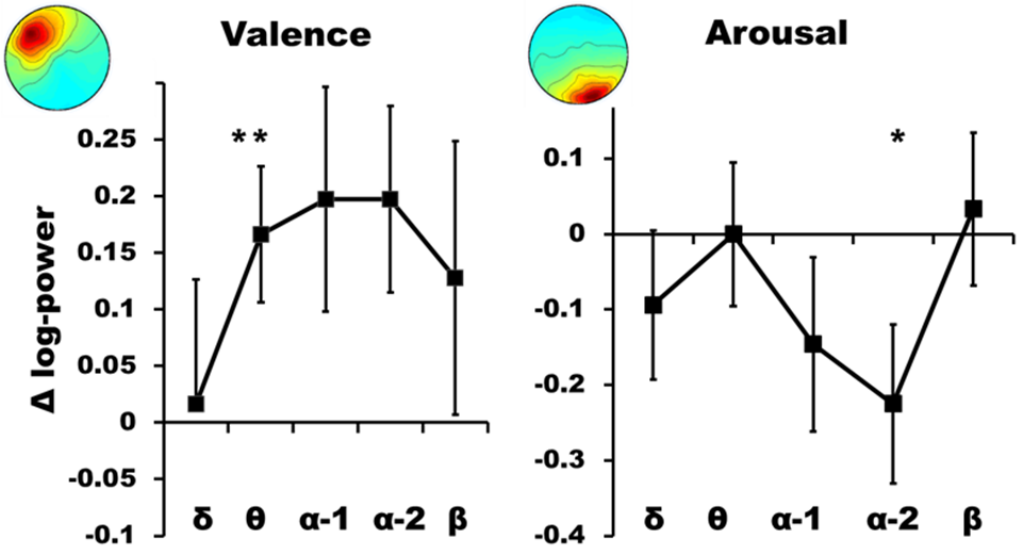

Fig. 3. Differences (in Δ log-power) plotted as a function of frequency range for cluster #3 (left: positive–negative) and cluster #10 (right: high–low). The bars depict standard errors. The asterisks indicate significant effects (*P < 0.05, **P < 0.01). Holm-corrected.

2.3.5 Discussion

The focus of this work was to examine the neurophysiological activations evoked during natural music-listening conditions. In order to get access to functionally distinct brain processes related to music-evoked emotions, we decomposed the EEG data by using ICA. The advantage in interpreting ICs lies in its unmasked quality, making it easier to disentangle and identify EEG patterns, which might have remained undetectable when using standard EEG techniques (Makeig et al., 2004; Onton and Makeig, 2006; Jung et al., 2001). ICA denoises and provides an EEG signal considerably less influenced by non-brain artifacts, making source analysis more precise. Thus, the EEG results we revealed here are closely related to neurophysiological processes. In this study, we revealed a valence–arousal distinction during music listening, which is clearer as has been reported in previous studies of this type. In the following, the main findings will be discussed in a broader context.

2.3.5.1 Brain sources underlying music-evoked emotions

Consistent with a great body of studies on music listening (e.g. Platel et al., 1997; Brown et al., 2004; Schmithorst, 2005), we found multiple neural sources contributing to the emergence of music-evoked emotions. In fact, the IC clusters we revealed here largely overlap with the ones found in a previous ICA study in which musical excerpts were manipulated in mode and tempo (Lin et al., 2014). Moreover, we revealed distinct subcortical sources, a finding supported by many functional imaging studies on music and emotions. Limbic as well as paralimbic structures are known to be involved in music listening (Brown et al., 2004), and are strongly related to pleasure and reward (Blood et al., 1999; Blood and Zatorre, 2001; Koelsch et al., 2006; Koelsch et al., 2008; Salimpoor et al., 2011; Salimpoor et al., 2013). In addition, the thalamus and anterior cingulate cortex (ACC) constitute a considerable part of the arousal system (Paus, 1999; Blood and Zatorre, 2001). Furthermore, also valence has frequently been ascribed to such subcortical structures, namely to the amygdala, parahippocampus, ACC, insular cortex and orbitofrontal cortex (Khalfa et al., 2005; Baumgartner et al., 2006b; Mitterschiffthaler et al., 2007; Green et al., 2008; Brattico et al., 2011; Liégeois-Chauvel et al., 2014; Omigie et al., 2014).

Altogether, the mesolimbic reward network has recently been associated with valence during continuous music listening (Alluri et al., 2015). Worthy of mention, a recent study also using a data-driven approach, namely one based on inter-subject correlations, was able to identify specific moments during music listening and thereby associate valence and arousal with responses of subcortical regions, such as the amygdala, insula and the caudate nucleus (Trost et al., 2015).

In line with many music-related EEG studies (Schmidt and Trainor, 2001; Tsang et al., 2001; Altenmüller et al., 2002; Sammler et al., 2007; Lin et al., 2010; Mikutta et al., 2012; Tian et al., 2013; Lin et al., 2014), we identified important contributing sources in the frontal lobe. In fact, several frontal regions are known to be involved in music processing, such as the motor- and premotor cortex (BA 4/6) in rhythm processing (Popescu et al., 2004), and the middle frontal gyrus in musical mode and tempo processing (Khalfa et al., 2005). In general, the medial prefrontal cortex is strongly associated with emotional processing (Phan et al., 2002). However, although dipoles are frequently found around the frontal midline (Lin et al., 2010; Lin et al., 2014), here we revealed two frontal clusters slightly lateralized on either side. This finding has previously been reported in auditory processing and working memory studies (e.g. Lenartowicz et al., 2014; Rissling et al., 2014). In contrast, the clusters we revealed around the fronto-central region and the precuneus overlap with the ones previously reported in music-related EEG studies (Lin et al., 2010, 2014). According to functional imaging studies, the inferior parietal lobule (BA 7) also contributes to musical mode (major/minor) processing (Mizuno and Sugishita, 2007), and the precuneus has been associated with the processing of (dis)harmonic melodies (Blood et al., 1999; Schmithorst, 2005).

Finally, several contributing neural sources were identified in the posterior portion of the brain. Similar posterior scalp maps have previously been reported in many music-related EEG studies focusing on ICs (Cong et al., 2013; Lin et al., 2014), even at 50 the level of single channels (Baumgartner et al., 2006a; Elmer et al., 2012). This is not surprising, considering the robust finding of occipital and cerebellar structures being active during music listening (Brown et al., 2004; Schmithorst, 2005; Baumgartner et al., 2006b; Chapin et al., 2010; Koelsch et al., 2013). The cerebellum is (together with sensorimotor regions) involved in rhythmic entrainment (Molinari et al., 2007; Chen et al., 2008; Alluri et al., 2012), whereas occipital regions and also the precuneus/cuneus contribute to visual imagery (Fletcher et al., 1995; Platel et al.,

1997), both psychological mechanisms proposed to be partly responsible for giving rise to musical emotions, as conceptualized in the BRECVEM model proposed by Juslin (2013).

2.3.5.2 Arousal and posterior alpha

The right posterior area of the brain, including occipital and cerebellar structures, appeared to be crucial in mediating arousal during music listening as indicated by a suppression of upper alpha power. In general, alpha power has frequently been related to affective processing (Aftanas et al., 1996; Aftanas and Golocheikine, 2001) and various aspects of music processing (Ruiz et al., 2009; Schaefer et al., 2011). Alpha power is inversely related to brain activity (Laufs et al., 2003a,b; Oakes et al., 2004), thus a decrement reflecting stronger cortical engagement. This suppression effect in connection with arousal has been reported in several studies (for a review see Foxe and Snyder, 2011), and has again been confirmed by our findings (Figure 3). However, the alpha suppression effect we revealed here was only apparent in the upper frequency range. A similar finding was reported by a recent EEG study employing graph theoretical analyses on the basis of EEG data. In this study, enhanced synchronization in the alpha-2 band during music listening was observed (Wu et al., 2013). However, in addition to this alpha suppression there was also a (non-significant) suppression in delta activity. This is consistent with a previous ICA finding showing differential delta power in response to highly arousing music (Lin et al., 2010).

Alpha oscillation, especially originating from parieto-occipital regions, drives an inhibitory process in primarily uninvolved brain areas (such as visual areas) (Fu et al., 2001; Klimesch et al., 2007; Jensen and Mazaheri, 2010; Sadaghiani and Kleinschmidt, 2013) and is related to internally directed attention constituting mental states such as imagery (Cooper et al., 2003; Cooper et al., 2006) or a kind of roping into the music as proposed by Jäncke et al. (2015). In conclusion, low-arousing music appears to provide a promoting condition for visual imagery.

2.3.5.3 Valence and frontal theta

The left frontal lobe appeared to be crucial in mediating valence during music listening as indicated by differential theta power. Happiness appeared to be associated with an increase in theta frequency power. In general, theta power has not only been linked to aspects of working memory and other mnemonic processes (Onton et al., 2005; Elmer et al., 2015) but also emotional processing (Aftanas and Golocheikine, 2001), especially in the case of theta power originating from the ACC (Pizzagalli et al., 2003). In line with our results, increased frontal theta power has been reported in response to positively valenced music, such as in music inducing pleasure or joy (Sammler et al., 2007; Lin et al., 2010). Even though we revealed several dipoles along the midline, here the effect in the theta frequency range was principally linked to a frontal cluster slightly lateralized to the left hemisphere. This left-sided hemispheric dominance is consistent with previous reported power asymmetry in frontal regions in connection with positively valenced music, at least in the alpha frequency range (Schmidt and Trainor, 2001; Tsang et al., 2001). Worthy of mention, there was also a trend at this area pointing to differences in the alpha frequency range (Figure 3). The involvement of alpha (together with theta power) in the context of processing valenced stimuli has recently been revealed in an intracranial EEG study (Omigie et al., 2014). However, these differences here did not reach statistical significance (alpha-1: P=0.075; alpha-2: P=0.037) after correction for multiple comparisons. Furthermore, this increase in theta power is also linked to a (non-significant) increase in beta activity. This is in line with the previous ICA study by Lin et al. (2014) relating differential beta activity over the medial frontal cortex to music with major mode.

2.3.5.4 Lateralization effects and emotion models

In the past decades, emotions have principally been discussed on the basis of neurophysiological models postulating functional asymmetries of arousal and valence. Regarding the valence dimension, it has been proposed that the left frontal lobe contributes to the processing of positive (approach) emotions, while its right-hemisphere counterpart is involved in the processing of negative (avoidance) affective states (Davidson et al., 1990). In line with this model, our results also suggest an association between positive emotions and the left-sided frontal areas. However, although our analyses also yield a right-sided frontal cluster, our findings

do not confirm an effect of negative emotion there. A reason for this discrepancy may be due to the fact that sadness in the context of music is rather complex involving moods and personality traits and situational factors (Vuoskoski et al., 2012; Taruffi and Koelsch, 2014). Therefore, music-induced sadness does not lead to withdrawal in the same manner as it does in a non-musical context. In fact, sadness induced by music may be experienced as pleasurable (Sachs et al., 2015; Brattico et al., 2016), which is why some authors have also argued to consider such emotions as vicarious (Kawakami et al., 2013, 2014). Thus, the approach-withdrawal model that was proposed on the basis of rather everyday emotions does not seem to be entirely suitable for describing music-evoked emotions. Heller (1993) proposed a similar model, however, incorporating the arousal dimension. In addition to the frontal lobe modulating valence by either hemispheric side, this model assumes that arousal is modulated by the right parieto-temporal region, a brain region we also identified in our study as being associated with music-evoked arousal. Still in line with this model, our analyses revealed another right lateralized cluster (R temporal–occipital) close to the area described in the model.

2.3.5.5 Limitations

Similar to many studies on emotions (Schubert, 1999; Schmidt and Trainor, 2001; Chapin et al., 2010; Lin et al., 2010), we investigated affective responses within a two-dimensional framework. Although our findings are to some extent transferable to more general non-musical emotions, our setting does not allow capturing more differentiated emotions such as the aesthetic ones characterized by the GEMS (Zentner et al., 2008).

In order to take into account the idiosyncratic nature of music-listening behavior, our experimental conditions were directly manipulated on the affective level, entailing exposure of non-identical stimuli sets. Although the subject-wise selected stimuli demonstrated physical comparability among conditions, our experimental setting does not permit to reasonably determine the impact of acoustic features on emotional processing.

2.3.6 Conclusion

By applying ICA, we decomposed EEG data recorded from subjects during music listening into functionally distinct brain processes. We revealed multiple contributing neural sources typically involved in music and emotion processing, namely around the thalamic–limbic and orbitofrontal domain as well as at frontal, frontal–parietal, parietal, parieto-occipital, temporo-occipital and occipital regions. Arousal appeared to be mediated by the right posterior portion of the brain, as indicated by alpha power suppression, and valence appeared to be mediated by the left frontal lobe, as indicated by differential theta power. These findings are partly in line with the model proposed by Heller (1993), arguing that the frontal lobe is involved in modulating valenced experiences (the left frontal hemisphere for positive emotions) whereas the right parieto-temporal region contributes to the emotional arousal. The exciting part of this study is that our results emerged 'blindly' from a set of musical excerpts selected on an idiosyncratic basis.

2.3.7 Funding

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Conflict of interest. None declared.

2.3.8 References

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3. Discussion

3.1 Synopsis

With aid of various EEG techniques, this thesis determines the contribution of particular processing stages and component processes to specific phenomena within the scope of auditory research. More specifically, it provides scientific contribution to the topic of auditory processing and interwoven affective processes.

By means of a passive oddball paradigm, study 1 provides first evidence showing that in a passive listening condition rather a cognitive than a sensory mechanism contributes to the phenomenon of AP. The study does not reveal any group differences in the MMN component, suggesting comparability regarding the early stage of pre-attentive auditory processing. Compared to controls, however, subjects with AP exhibit a reduction in the P3a responses reflecting a more efficient and parsimonious allocation of cognitive demands during tone processing. Altogether, this is in line with the growing consensus (Elmer, Hänggi, Meyer, & Jäncke, 2013; Elmer, Sollberger, Meyer, & Jäncke, 2013; Levitin & Rogers, 2005; Zatorre et al., 1998; Levitin, 1994), considering the later-occurring and cognitively based processing stage as the crucial operation for AP. Since the P3a component is known to also reflect early multimodal processing (Jancke, et al., 2012; Boll & Berti, 2009), as multimodal brain regions also contribute (i.e., temporal–parietal junction; Knight, et al., 1989), the revealed facilitation effect is possibly driven by multiple codes for tones (i.e., verbal, auditory imagery, sensorimotor cues) additionally available in AP subjects, supporting the widespread view that AP ability relies on multiple mental codes (Hantz et al., 1992; Zatorre et al., 1998; Zatorre & Beckett, 1989; Klein et al., 1984). However, the P3a reduction is especially evident in the processing of whole tone categories referring to semitones used in Western music. These pitch types correspond to the ones we are usually exposed to and thus the ones especially acquired during early musical training within the sensitive period. Therefore, this interaction effect reflects an influence of early musical exposure on AP, a finding already reported on several occasions (e.g., Deutsch et al., 2006; Gregersen et al., 2001; Meyer et al., 2011; Ohnishi et al., 2001). Further compatible with this early musical exposure effect on AP are the revealed positive correlations

between the P3a amplitudes and the age of commencement of musical training in AP subjects. Thus, the later AP subjects start their musical training the weaker their P3a amplitudes get diminished, reflecting a loose in efficiency increasing with elapsed AP-acquirable time. However, study 1 only reveals correlations in the conditions in which deviant tones are mistuned, suggesting that AP subjects are more vulnerable to tones that have not explicitly been acquired during the sensitive period. A certain vulnerability to mistuned tones in AP subjects is supported by a study showing performance impairment (i.e., reaction time, accuracy) in identifying musical intervals in an out-of-tune reference condition (Miyazaki, 1992), but also by anecdotal reports (see Levitin & Rogers, 2005), suggesting affective effects in terms of an aversion in response to mistuned tones.

Study 2 captures the brain processes underlying music-evoked emotions by using high-density EEG recordings from subjects listening to music under ecologically valid circumstance. The study optimizes ecological validity of a music-listening laboratory condition by, firstly, taking into account the idiosyncratic nature of music experiences (Gowensmith & Bloom, 1997; Juslin & Laukka, 2004; Zatorre, 2005). From a peer-assembled pool of various musical excerpts, study 2 matches for the EEG session subject-wise sets of excerpts regarding previous rating profiles (i.e., valence and arousal scales). However, the non-identical stimuli presented across subjects between the affective conditions (i.e., positively valenced versus negatively valenced; highly arousing versus lowly arousing) are still comparable regarding intensity (i.e., normalized amplitudes), the rhythmic (i.e., tempo), tonal (i.e., tonal centroid) and timbral (i.e., zero-crossing rate) structure, permitting to attribute revealed effects to the affective dimensions. Secondly, instead of using ERP-suitable material (i.e., short stimuli in length but high in frequency of occurrence), the study uses whole musical excerpts with sufficient length (i.e., 60 sec) that include specific temporal dynamics, enabling authentic music-evoked emotions to unfold (e.g., due violation/confirmation of established expectancies; Meyer, 1956; Sloboda, 1991).

Despite the highly diverse and relatively few stimuli, the study ensures optimal signal-to-noise ratio of the recorded EEG data by applying a powerful data-mining technique called ICA that decomposes the EEG data into temporally maximally independent contributors. With aid of a k-means cluster analysis calculated on the basis of a combination of the spatial (scalp topography and dipole location and

functional (spectra) characteristics of the independent components, study 2 “blindly” determines functionally distinct brain processes underlying emotions during natural music listening. Apart from multiple contributing sources typically involved in music and emotion processing, namely around the thalamic–limbic and orbitofrontal domain as well as at frontal, frontal–parietal, parietal, parieto-occipital, temporo-occipital and occipital regions, these analyses reveal a valence–arousal distinction during music listening, which is clearer as has been reported in previous studies of this type. According to the findings, arousal appears to be mediated by the right posterior portion of the brain (i.e., occipital and cerebellar structures) as is indicated by alpha power suppression. This is in line with studies relating arousal power to affective processing (Aftanas et al., 1996; Aftanas & Golocheikine, 2001) and various aspects of music processing (Ruiz et al., 2009; Schaefer et al., 2011) as well as with an alpha suppression effect in connection with arousal (Foxe & Snyder, 2011). On the other hand, valence appears to be mediated by the left frontal lobe, as indicated by differential theta power. This is in line with previous findings on theta power in connection with emotional processing (Aftanas & Golocheikine, 2001) and specifically in response to positively valenced music (Sammler et al., 2007; Lin et al., 2010).

In overall, these findings are partly compatible with an older model proposed by Heller (1993), arguing that right parieto-temporal region contributes to the emotional arousal whereas the frontal lobe is involved in modulating valenced experiences. According to this model, the left frontal side contributes to the processing of positive emotions, whereas the right one contributes to the processing of negative emotions. Whereas study 2 replicates this linkage between the left-sided frontal lobe and positive emotions, it does not confirm an effect of negative emotion at the right-hemisphere counterpart. A reason for this discrepancy may be due to the fact that sadness in the context of music is rather complex involving moods and personality traits and situational factors (Vuoskoski et al., 2012; Taruffi & Koelsch, 2014). Therefore, music-induced sadness does not lead to withdrawal in the same manner as it does in a non-musical context. In fact, sadness induced by music may be experienced as pleasurable (Sachs et al., 2015; Brattico et al., 2016), which is why some authors have also argued to consider such emotions as vicarious (Kawakami et al., 2013, 2014). Thus, approach-withdrawal models (see Davidson et al., 1990; Heller, 1993) proposed on the basis of rather everyday emotions do not seem to be entirely suitable for describing music-evoked emotions.

To date, it is still under discussion whether concepts designed for everyday (i.e., utilitarian) emotions can also be applied to an aesthetic context such as music, and to what extent the two affective dimensions are adequate to describe the richness of emotional experiences induced by music (Zentner et al. 2008). However, a study by Vuoskoski et Eerola (2011) revealed that overall consistency of ratings (i.e., intraclass correlations and Cronbachs alpha) was the highest in the case of the dimensional model which outperformed the other two models (i.e., GEMS and discrete model) in the discrimination of musical excerpts. Furthermore, the authors performed a principal component analysis and revealed that 89.9% of the variance in the mean ratings of all the scales was accounted for by two components that could be labelled as valence and arousal.

3.2 Concluding remarks and future directions

The two research topics of this dissertation are promising in enlightening the auditory system in connection with affective processing. Music listening as well as music-induced emotions is a universal, into which insights contribute to the knowledge of human nature. As already pointed out, research on AP is instructive, yielding far-reaching results. AP not only has evolutionary and ontogenetic significance (Hauser & McDermott, 2003; Saffran & Griepentrog, 2001), but also contributes to the better understanding of plasticity in the auditory system or interactions between experiential, maturational and genetic factors during general cognitive development (Zatorre, 2003). Of significance is the fact that AP develops in a specific maturational stage, in which also language is acquired (Gervain et al., 2013; Russo, et al., 2003; Miyazaki, 1988) and hierarchically higher (interfering) cognitive abilities are not emerged yet (i.e., unidimensional instead of multidimensional thinking; Chin, 2003), corresponding to a period during which the brain exhibits a high degree of plasticity (Schlaug, 2001). Related to this, AP shows numerous overlapping features with other developmental conditions (i.e., synesthesia) and developmental disorders (i.e., autism spectrum disorder and Williams syndrome). Synesthesia frequently appears in subjects with AP and/or autism spectrum disorder (Bouvet et al., 2014; Mottron et al., 2013; Neufeld et al., 2013). On the other hand, subjects with autism or Williams syndrome are frequently reported to possess AP in terms of a savant skill (Bonnel et al., 2003; Brenton et al.,

2008; Crespi, 2013; Heaton et al., 2008; Lenhoff et al., 2001), and AP subjects are known to exhibit more autistic traits than controls (Brown et al., 2003; Dohn et al., 2012). Further overlapping features between AP subjects and developmentally delayed populations are genes (Brown et al., 2003) and brain architectures, in the sense of a common hyperconnectivity between relevant brain regions underlying a kind hyperfunctioning in terms of a giftedness (Loui et al., 2011, 2012).

The inferred vulnerability to mistuned tones in subjects with AP (study 1) might reveal a further insightful overlapping feature. Specific types of auditory abnormalities have already been reported in autism spectrum disorder and Williams syndrome, namely in terms of an aversion to particular everyday life sounds (e.g., cheering crowd, thunder, dog barking, sneezing) that are not normally considered to be aversive (Levitin, 2005; Levitin et al., 2005; O'Connor, 2012; Rosenhall et al., 1999; Stanutz et al., 2014). A similar phenomenon has also been reported in synesthesia reflecting strong negative affective reactions to stimuli mismatching the synesthetically induced attributes (Callejas et al. 2007). This vulnerability effect together with the anecdotal evidence of AP subjects responding aversively to mistuned tones (Levitin & Rogers, 2005), suggests a further common denominator among developmental conditions. However, further research is required to verify an AP-specific auditory aversion. Providing empirical findings on this possible phenomenon might be fruitful due to its interlinkage with the several fundamental topics, of which an investigation might enable access to a possible underlying root, gaining insights into cognitive-affective development in connection with brain plasticity.

The automatic processing of emotional experiences underlying auditory aversion could be measured using an affective priming paradigm that involves the sequential presentation of two valenced stimuli (Fazio et al., 1986; Klauer & Musch, 2001). In this context, subjects are required to judge as quickly and accurately as possible whether targets are pleasant or unpleasant, whereby valenced primes (i.e., out-of-tune versus in-tune tones) precede the targets. The primes are either affectively related or affectively unrelated to the targets. Behavioral responses are known to become faster on trials for which the primes and the targets are congruent. By contrast, responses become slower on incongruent trials. This discrepancy is called the affective priming effect and reliably indicates the extent of the involved emotional experience. Several studies have applied this paradigm in combination

with ERP recording by evaluating the so-called N400 component as an electrophysiological correlate of affective processing. The N400 component is a negative-going deflection observed around 400 msec after target onset (Kutas & Hillyard, 1980). Enhanced N400 responses are observed in response to semantically incongruent targets (Kutas & Federmeier, 2011). Within the framework of affective priming paradigm, however, the N400 component is used as an index of processing affective mismatches between primes and targets (Eder et al., 2011; Goerlich et al., 2011; Steinbeis & Koelsch, 2011; Zhang et al., 2006, 2010). Finally, the two EEG techniques used for this thesis could be combined. Thus, the N400 response could be derived from particular independent components, improving the signal-to-noise ratio and additionally providing access to cortical sources.

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Curriculum Vitae

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Jancke L, **Rogenmoser L**, Meyer M, & Elmer S. (2012). Pre-attentive modulation of brain responses to tones in coloured-hearing synesthetes. *BMC Neuroscience, 13*(1), 151. doi: 10.1186/1471-2202-13-15.

SCHOLARSHIPS

2016-2018	Early Postdoc.Mobility Fellowship Swiss National Science Foundation (SNSF) Project: **The acoustic startle reflex as objective measure for tinnitus distress** (grant no. P2ZHP1_168587 to LR) Supervisor: Ph.D., D.Sc. Josef Rauschecker Laboratory of Integrative Neuroscience and Cognition within the Department of Neuroscience at Georgetown University Medical Center (Washington DC, USA)
2015-2016	Doc.Mobility Fellowship Swiss National Science Foundation (SNSF) Project: **Auditory aversion in subjects with absolute pitch** (grant no. P1ZHP1_158642 to LR) Supervisor: M.D. Ph.D. Gottfried Schlaug

Music and Neuroimaging Laboratory within the Department of Neurology at Beth Israel Deaconess Medical Center and Harvard Medical School (Boston, USA)

PRESENTATIONS

Talks

2015/11 **Widening the lens on Auditory Function: Exploring perspectives on Auditory Processing and Affective Response.** Invited talk at the Rauschecker lab, Georgetown University, November 23th, Washington DC, USA

2015/10 **Melody discrimination task reveals functional activation deficits in a left posterior inferior frontal region in tone-deaf compared to typically developing individuals.** Nanosymposium at the Society for Neuroscience (45th Annual Meeting), October 17th-21th, Chicago, USA

2015/02 **Musik und Psyche**. Invited talk at the „Privatklinik Wyss“, February 12th, Münchenbuchsee, Switzerland

2014/10 **Music and the brain**. Invited Talk at the Brain Festival 2014, October 7th, Institute Le Rosey in Rolle, Switzerland

2014/03 **Synästhesie – Wenn Töne Farben induzieren**. Talk organized by the Brainfair Zurich 2014, booked by the following school classes:

March 14th: Sekundarschule Rümlang-Oberglatt, Rümlang, Switzerland

March 13th: Lycée Français Marie Curie de Zurich, Glockhausen, Switzerland

March 3th: Kantonsschule Limmattal, Urdorf, Switzerland

2014/05 **Evidence for Early Cognitive Facilitation in Absolute Pitch**. Talk at the ZNZ PhD Retreat 14, May 1th-3th, Clinic Valens, Switzerland

2014/03 **Absolute Pitch: A Cognitive Phenomenon**. Talk at the FameLab, March 19th, ETH Zurich, Switzerland

Posters

2016/06 **Rogenmoser L**, Kernbach J, Schlaug G, & Gaser C (2016). *Keeping brains young with music*. Poster at the Organization for Human Brain Mapping, June 26th-18th, Geneva, Switzerland

2016/01 **Rogenmoser L**, Li C, & Schlaug G. (2016). *How absolute pitch reacts to mistuned tones and changes with age.* Poster at Northeast Music Cognition Group meeting, January 16th, Harvard University, Cambridge, USA

2015/06 **Rogenmoser L**, Elmer S, & Jäncke L. (2015). *Independent components underlying music-evoked emotions*. Poster at the Organization for Human Brain Mapping, June 14th-18th, Honolulu, Hawaii, USA

2014/11 **Rogenmoser L**, Elmer S, & Jäncke L. (2014). *Decoding music-evoked emotions from brain activity*. Poster at the Society for Neuroscience (44th Annual Meeting), November 15th-19th, in Washington DC, USA

2014/09-10 **Rogenmoser L**, Elmer S, Kühnis J, & Jäncke L. (2014). *Three minutes of resting state is enough to predict absolute pitch performance*. Poster at the Resting states and state dependent information processing in health and disease conference, September 28th- October 1th, Centro Stefano Franscini, Monte Veritá, Ascona, Switzerland

2014/09 **Rogenmoser L**, Elmer S, & Jäncke L. (2014). *Decoding music-evoked emotions from brain activity*. Poster at the Symposium ZNZ (Neuroscience Center Zurich), September 11th, University of Zurich/ETH Zurich, Switzerland

2014/05-06 **Rogenmoser L**, Elmer S, & Jäncke L. (2014). *Absolute pitch possessors show early cognitive facilitation during passive listening: Evidence from the P3a component*. Poster at the Neuroscience and Music V, May 29th-June 1th, Dijon, France

2014/05 **Rogenmoser L**, Elmer S, & Jäncke L. (2014). *Absolute pitch possessors show early cognitive facilitation during passive listening: Evidence from the P3a component*. Poster at the LiMaDoko (LizentiandInnen-Materstdudiernden-Doktorierenden-Kongress), May 22th, Departement of Psychology, University of Zurich, Switzerland

2013/11

Rogenmoser L, Elmer S, & Jäncke L. (2013). *Pre-attentive tone processing in colored-hearing synesthetes*. Presented at the 17th EEGLAB Workshop, November 15th-18th, in La Jolla, USA

Oechslin M, **Rogenmoser L**, Kuhn-Rahloff C, Jäncke L, Meyer M, & Neukom M. (2013). *The doppler effect as a sufficient cue for the perception of dangerousness related looming auditory signals*. Poster at the Society for Neuroscience (43th Annual Meeting), November 9th-13th, in San Diego, USA

Rogenmoser L, Elmer S, & Jäncke L. (2013). *Pre-attentive tone processing in colored-hearing synesthetes*. Poster at the Society for Neuroscience (43th Annual Meeting), November 9th-13th, in San Diego, USA

2013/09

Rogenmoser L, Elmer S, & Jäncke L. (2013). *Pre-attentive tone processing in subjects with absolute pitch*. Poster at the Symposium ZNZ (Neuroscience Center Zurich), September 13th, University of Zurich/ETH Zurich, Switzerland

Rogenmoser L, Elmer S, & Jäncke L. (2013). *Pre-attentive tone processing in colored-hearing synesthetes*. Poster at 45th European Brain and Behaviour Society Meeting, September 6th-9th, in Munich, Germany

2012/05

Rogenmoser L, Elmer S, & Jäncke L. (2012). *Pre-attentive binding of tones and colors in the auditory cortex of synesthetes*. Poster at the LiMaDoko (LizentiandInnen-Materstdudiernden-Doktorierenden-Kongress), May 31th, Departement of Psychology, University of Zurich, Switzerland

AD HOC REVIEWING

Neuropsychologia

Plos One

Music Perception

NeuroReport

Cogent Psychology